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Ichthyofaunal and dietary analysis of sympatric piscivores in a Chesapeake Bay littoral zone: Including bioenergetic models of growth and diel temperature sanctuary use

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Ichthyofaunal and Dietary Analysis of Sympatric Piscivores in a Chesapeake Bay Littoral Zone: Including Bioenergetic Models of Growth and Diel Temperature Sanctuary Use

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Christian H. Hager
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This dissertation is submitted in partial fulfillment of
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DEDICATION

To my home.

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ABSTRACT

The ichthyofaunal community of a partially vegetated mesohaline Chesapeake Bay littoral zone is described from April through November in the first part of this dissertation. Faunal assemblages at various trophic levels were sampled using two seine gears, a small seine that sampled 352 m^2 and a 914m commercial haul-seine that sampled 144,473 $m^{2.}$ The small seine collected 32 finfish species. The larger gear captured 31 finfish species, including 17 that were not collected by the prey seine. Sampled diversity was greater but fish densities were similar to those determined by previous flume-net , drop ring, and otter trawl surveys in the same littoral zone. Nocturnal samples of upper level fishes far exceeded daylight samples and piscivore abundance and size distribution varied seasonally. The second portion of the work focused on the diet of striped bass, bluefish, and weakfish collected. These sympatric predators were the most abundant piscivores sampled in the littoral zone and gut content showed greater diversity and dependence on benthic prey resources (primarily crustacean) than previous Chesapeake Bay diet studies. The importance of pelagic prey increased with age across species in accordance with many previous works. The third section contains bioenergetic models that predict piscivore growth based nocturnal gut content and estimated consumption. Based on growth rate comparisons with fishes collected randomly from across the bays habitats, models predict that bluefish and weakfish feeding in littoral zones attain better growth rates. Striped bass are not metabolically suited to warm littoral waters and due to reduced consumption and physiological stresses models predict they experience declining condition during such physical conditions. Models also examined the bioenergetic consequences of seeking thermal sanctuary in deeper surrounding waters during daylight hours. Predicted outcomes illustrate how important species-specific metabolisms and habitat-specific seasonal alterations in physical parameters and prey resource acquisitions are to fish health. Predictions suggest that these parameters need to be considered at an age-specific level in spatial assessments of essential fish habitats.

Ichthyofaunal and Dietary Analysis of Sympatric Piscivores in a Chesapeake Bay Littoral Zone: Including Bioenergetic Models of Growth and Diel Temperature Sanctuary Use

CHAPTER 1. PROJECT OVERVIEW, OBJECTIVES, SITE DECRIPTION, AND SAMPLING METHOD JUSTIFICATION

PROJECT OVERVIEW AND INTRODUCTION

Approximately 40% of the Chesapeake Bay, the largest estuary in the continental United States, consists of shallow water habitats less than two meters deep (Spinner, 1969) which are collectively referred to as littoral zones. Historically, these zones contained a diversity of overlapping intertidal and subtidal habitats including fringing marshes, meadows of submerged aquatic vegetation (SAV), intertidal mudflats, and sandy shoals that created a dynamic mosaic for trophic exchanges serving a wide variety of species in different capacities at different stages of development (Cicchetti, 1998). Unfortunately, anthropogenic and natural influences have altered littoral habitat composition, notably reducing the extent of SAV coverage (Kemp et al., 1983) and surrounding marshes.

Habitat differences in prey biomass and availability alter trophic energy acquisition of predators and affect these fishes' condition (Lankford and Targett, 1994, 1997; Grecay, 1991; Grecay and Targett, 1996 a, b). Increased diversity of lower level prey provided in such habitats expands feeding niches available to consumers thus providing predators with energetic advantages (Harding and Mann, 1998). Numerous investigators have documented seagrass habitats for their high levels of primary and secondary production (Wetzel and Penhale, 1983; Dennison et al., 1993) and in most studies these grasses have been found to increase icthyofaunal species richness and abundance (Heck and Orth, 1980). There is substantial literature on the effects of seagrasses in providing refugia from predation (Orth et al. 1984; Heck and Thoman, 1981; Vince et al. 1976). In fact the fishes and crustaceans that inhabit littoral zones may be capable of integrating habitat profitability for feeding with risk of predation, thus optimizing trophic and refuge benefits (Werner et al. 1983). Others works have recognized tidal marshes for their trophic and habitat contributions to fishes (Gunter, 1956, 1961; Nixon and Oviatt, 1973; Subrahmanyam and Drake, 1975; Daibner, 1977; Weinstein, 1979; Boesch and Turner, 1984; Currin et al., 1984). It has virtually become an article of faith among estuarine scientists and environmental managers that the diverse primary producers found in littoral zones and the food and refuge functions they provide are important in sustaining estuarine fisheries species (Boesch and Turner, 1984).

Littoral zones containing sub and intertidal grasses have long been recognized for their contributions to the composition and abundance of fish assemblages (Petersen, 1918). In some regions the icthyofaunal abundance within vegetated habitats can be twice that found in surrounding unvegetated intertidal habitats (Edgar and Shaw 1995a). Theoretically, seagrasses expand the availability of lower level trophic resources, thus increasing total fish production through enhanced food availability (Lubbers et al., 1990). Seagrass habitats are well documented as being extremely important to crustaceans (Howard et al., 1989; Edgar et al., 1994) and in some grassbeds, crustaceans form the dominant dietary component of small fishes (Edgar and Shaw, 1995b, Adams, 1976; Brook, 1977) and thus may serve as an important energetic link between primary production and trophic export by transient upper level fishes. Because so little is known about the trophic contributions these zones and their surrounding marshes make to larger upper level fishes (Knieb, 1997) limited evidence is available to support or refute this hypothesis (Edgar and Shaw, 1995b).

Over the past several decades the Chesapeake and its adjoining bays of the Delmarva Peninsula have experienced a drastic decline in seagrass coverage (Orth and Moore, 1983, 1984), due to disease (Cottam and Munro, 1954; Rasmussen, 1975), meteorological events, (Orth et al., 2002) and declining water quality. Littoral grasses are known to provide food and refugia to many species including juvenile piscivores (Briggs and O'Conner, 1971; Chao and Musick, 1977; Ayvazian et al. 1992; Murdy et al. 1997). Littoral grasses are so important to crustaceans that the biomasses of the two are positively correlated (Howard et al., 1989; Edgar et al., 1994). Small fish production is in turn highly correlated with crustacean production (Edgar ad Shaw, 1995a). Littoral grass reductions may have limited the Bay's provision of suitable nursery areas and production of epifaunal prey to the point that it is limiting piscivore production. Carpenter (1988) recognized how such ecological disturbances at lower levels can permeate throughout the food web of freshwater systems, thus linking water quality issues with fisheries production.

Striped bass, bluefish, and weakfish range along most of the eastern seaboard of the United States and support valuable fisheries throughout their ranges (Wilk, 1979; Mercer, 1983; Mid-Atlantic Fishery Management Council et al., 1989). Each of these ecologically, economically, and recreationally important fishes rely upon estuarine resources and this reliance is one of the primary economic reasons for the preservation of such systems (Odum, 1971). These fish are the dominant predatory finfish in the Chesapeake Bay (Hartman and Brandt, 1995a) where they significantly contribute to numerous fisheries (Seltzer et al., 1980; Mercer, 1985; MFMC et al. 1989). Striped bass and weakfish spawn within the confines of the Bay itself. Bluefish spawn offshore and young-of-the-year (YOY) immigrate into the Bay in the spring. Each species relies on the Bay's habitats at various life stages. The YOY and adults of all three species rely upon the estuary's littoral habitats for refugia and production of suitable prey resources. Adults metabolize consumed resources into growth and reproductive efforts. The dynamics of these species are of ecological interest not only because they span three families of fishes (*Moronidae, Pomatomidae, and Sciaenidae*) but also because they are often the top piscivorous predators in many estuarine systems (Chao and Musick, 1977; Friedland et al., 1988). As the principle apex predators, their dynamics and trophic impacts may alter the structure and function of lower levels in a top-down manner or their population dynamics may be affected in a bottom-up manner by alterations of productivity at the lower levels upon which they depend trophically (Carpenter et al., 1985; Carpenter, 1987).

As research accumulates, it is becoming increasingly obvious that system health and fisheries production is not solely a product of top-down or bottom-up controls. Maintaining sustainable harvest requires good stewardship of both mechanisms. It is a matter of historical fact that with the aid of technology, fish stocks can be over harvested. It is also becoming widely recognized that a large amount of trophically transferable lower level production is required to furnish desired biomass levels of important piscivores and that some habitats are more productive with regards to providing for these fishes than others. Expanding awareness as to how and where biomass is transferred in energetically rich littoral habitats will provide a greater understanding of the community structure, the habitat quality, the food supply, and ultimately the nutrient and sediment load boundaries that will encourage provision of sustainable harvest.

In this study, the importance of a vegetated mesohaline littoral zone to the growth of striped bass, bluefish, and weakfish was investigated. This project consisted of two overarching interacting goals. The first goal was to conduct the first large-scale temporal survey to date of predator and prey densities within a typical partially vegetated mesohaline littoral zone. The second goal was to construct bioenergetic models of striped bass, bluefish, and weakfish growth based on temporal consumption and environmental conditions. In order to accomplish these goals three major projects were undertaken. The purpose of the first project was to examine quantitatively the seasonal abundance, biomass, diversity, composition and density of fishes using a mesohaline vegetated littoral zone. The second project examined the seasonal habits, diet, and trophic overlap of striped bass, bluefish, and weakfish in the zone. The third, and final objective was to construct bioenergetic models that describe and quantify potential growth of these species based on average daily ration, to test the models' sensitivities, and to explore energy saving approaches that each fish may incorporate.

This dissertation is divided into four chapters. This chapter contains the project overview including a general introduction, background, justification, and objective summary. Chapter 2 is a faunal survey in which a small and large seine were used to simultaneously sample large icthyofauna and prey species. The area and species-specific efficiencies of each gear were determined. Monthly assemblage structure, abundance, biomass, and density of specimens were estimated. Length-weight regressions were calculated for species captured in significant numbers. Monthly diversity was examined through application of Margalef's diversity index. Diel differences in striped bass, bluefish, and weakfish abundance were statistically examined and bycatch and ecological impact associated with large haul-seine methods were discussed. Chapter 3 contains analyses of these upper level piscivores' stomach contents. Content was expressed as average mass per fish (S), gut fullness (gm prey/gm predator), % mass (W), % number (N), % frequency of occurrence (O), index of relative importance (IRI), and % IRI monthly. Cumulative prey curves were created for each predator to determine if diet was described fully, and diet overlap between piscivores was examined using Schoener's index (1970). Chapter 4 contains an individual based bioenergetics model for each of the three sympatric predators. Models simulate annual growth of an average sized fish of each species based on average daily ration. Fish size and consumption are based on field data. Sensitivities of the most influential model variables, according to literature review, are tested and potential energy savings provided by seeking thermal sanctuaries examined for effect on growth. Determining annual growth provides a means of simplifying seasonal trophic acquisitions and quantifies the habitat's contributions in terms of biomass production. Quantifying an average individual's growth based on environmental and trophic parameters determined through field investigations provides a medium that can be used to compare subsystem habitats with each other or with the system as a whole. Comparisons between various subsystem habitats will be provided for when the parameters controlling growth in these spatially explicit systems are determined in the future.

BACKGROUND, JUSTIFICATION AND PROJECT OBJECTIVES

Estuaries are energetically rich and highly productive ecotones where fresh and salt waters intersect and mix to provide essential resources and habitats to migratory and endemic species alike. The unique physiochemical environment provided results in high primary productivity and abundant energy at lower levels, which supports a diverse faunal community (Day, 1981). The physiochemical conditions, abundant prey resources, and vegetated littoral habitats that reduce predation risk of small fishes promote fish growth and make the regions suitable spawning grounds and nursery grounds (Joseph, 1973; Miller et al. 1984). The dependence of so many commercially, recreationally, and ecologically important fisheries on estuaries is one of the major economic reasons for preservation of these habitats (Odum, 1971).

The Chesapeake Bay and its tributaries form the largest estuarine system in the continental United States and support a large ichthyofaunal diversity (e.g. Hildebrand and Schroeder, 1928; Musick, 1972; Weinstein, 1985, Murdy et al., 1997) consisting of more than 267 species. The Chesapeake like all estuaries is a diverse and dynamic transition zone where marine and freshwater environments merge and interact. It serves as a nursery and growth area to resident and transient species (Horwitz, 1987; Murdy et al., 1997). The Chesapeake's species richness and its ecological importance are augmented by its large seasonal temperature changes and habitat diversity (Murdy et al., 1997).

The Chesapeake Bay once sustained a larger number of upper level piscivores that supported several healthy commercial fisheries (Hildebrand and Schroeder, 1928). Over the past 60 years, catch composition of the fisheries clearly evidences alterations to the estuary's faunal assemblage structure (Miller et al., 1996). Populations of many larger, higher priced species (i.e. piscivorous fishes) have been drastically reduced. This has resulted in an increased dependence upon and augmentation of the fishing pressures on more rapidly reproducing lower trophic level species such as blue crabs (*Callinectes sapidus*) and menhaden (*Brevortia tyrannus*). Changes in faunal assemblages are attributed to a number of factors including loss of essential fish habitats, water quality degradation, and overfishing and ultimately, a lack of effective management of these factors.

Understanding the factors that lead to declining upper level finfish stocks presents an extremely complex problem involving biological, physical, economic, and social factors. Fish recruitment is highly variable and population fluctuations make it difficult to distinguish between natural variations and those caused by man. Interactions between fish stocks, water quality, climate, and anthropogenic alterations to habitat and community structure are incompletely understood and have thus far been omitted from most management schemes. Traditionally, water quality, critical habitats, and fish population dynamics have been treated as separate management issues. However, the declines in some stocks despite stringent regulations to control harvest have emphasized the need to formulate a more holistic approach (Ault et al., 1999) that includes predator-prey interactions and habitat dependencies.

Understanding the factors that govern the movements and distributions of predator and prey is crucial to quantifying the trophic interactions that control piscivores' production (Buckel and Conover, 1997). It is well recognized that differences in prey biomass and availability alter trophic energy intake and affect predators' condition (Lankford and Targett, 1994, 1997; Hartman and Brandt, 1995b, d; Grecay and Targett, 1996b). An estuary's ability to produce a given predator is thus linked to its provision of appropriate prey. Prey production is dependent upon the quantity and quality of suitable habitats and trophic resources within the estuary. Large-scale reductions in the coverage of highly productive habitats within an estuary may have cascading effects throughout the trophic architecture of the system (Carpenter et al. 1985; Posey and Hines, 1991) significantly affecting production dynamics at the population and ecosystem level (Brandt et al., 1992).

The recent large-scale striped bass population recovery along the Atlantic coast has augmented concern over the impact this recovery has had on other possibly competing piscivores and prey species. Competition is known to influence spatial distribution (Werner and Hall, 1976; Hixon, 1980; Robertson, 1995), prey utilization (Werner and Hall, 1976; Persson, 1987), growth (Werner and Hall, 1976; Prout et al. 1990, Davis and Todd, 1998), and survivorship (Bystroem et al., 1998). Concurrent declines in bluefish landings with striped bass recovery (NMFS, 2004) led to hypothetical biotic competitive interactions. Field and laboratory data currently provides no evidence of competitive interactions between juvenile striped bass and bluefish (Buckel and McKown, 2002). Current research does, however, suggest that recovery may significantly affect prey resources, which are of commercial and recreational interest (Hartman, 2003). Recent diet analysis (Overton et al., 2000), examination of previously unpublished diet content (Griffin and Margraf, 2003) and archived scales isotope ratios (Pruell et al., 2003) indicate a significant increased reliance on benthic prey suggesting that significant changes in feeding behavior and/or feeding locations have occurred.

The findings of Hartman and Brandt (1995d) suggest that the Chesapeake Bay's production of upper level fishes is limited by the availability of suitable prey resources. In other systems the refugia and trophic resources provided by littoral habitats have been identified as being critical to piscivores at various life stages (Gunter, 1956, 1961; Nixon and Oviatt, 1973; Subrahmanyam and Drake, 1975; Daibner, 1977; Weinstein, 1979; Boesch and Turner, 1984; Currin et al., 1984). Chesapeake Bay littoral studies focussing on lower trophic levels and/or juvenile piscivores have provided increased evidence of prey abundance and diversity in these zones (Orth and Heck, 1980; Ryder, 1987; Boyton et al. 1981; Ayers, 1995; Buzzelli, 1996; Cicchetti, 1998, Wagner and Austin, 1999; Harding and Mann, 2000; Clark et al. 2003). A few studies have addressed the trophic reliance of piscivores on specific habitats within these zones such as oyster reefs (Harding and Mann, 2001b; Harding and Mann, 2003), sand bars and eelgrass beds (Lascara, 1981), salt marshes (Tupper and Able, 2000) and tidal creeks (Nemerson and Able, 2003) these studies have provided evidence of increased diet breadth and reliance on benthic prey resources.

Unfortunately, the quality and quantity of littoral habitats in the Bay have been severely degraded since the 1930's. Habitat alterations may have reduced prey production and availability thus reducing the system's ability to support or produce historic levels of piscivore biomass. If this hypothesis is correct and quantity and quality of shallow water habitats is linked to the production of upper level fish biomass through the trophic resources they collectively produce formerly separate management issues of water quality and upper level productivity merge. This hypothesis also provides an ecological explanation for the resource limitations found by Hartman and Brandt (1995d). There is clearly a need to further investigate the role these habitats play in piscivore production and quantify energetic contributions (Nixon and Oviatt, 1973; Subrahmanyam and Drake, 1975; Bozeman and Dean, 1980; Currin et al., 1984; Weinstein et al., 1984).

Magnuson-Stevens (1996) recognizes the importance of habitat losses and their previously unquantified effects on the production of upper level fishes and recommends that such habitats referred to as "essential habitats" be identified and their contributions quantified. The connection between vegetated habitat and the production of upper level fishes is supported by several geological and historical observations. First, the Bay's littoral habitats cover approximately 40 % of the Bay's area (Spinner, 1969) and the majority of these were historically vegetated habitats that produced and contained a large biomass of potential prey species. Second, concurrent with loss of these habitats was the overfishing of many upper level fishes. Despite adequate regulations to provide for stock recoveries many of these once plentiful upper level fish populations have not recovered suggesting that system alterations had occurred that now limited stock recovery. The reliance of fishes upon habitat and the quantity and quality of the resources it provides is becoming more apparent (Peters and Cross, 1992; Edgar and Shaw 1995 a, b; Harding and Mann, 2001, Harding and Mann, 2003; Walter et al. 2003; Schaffler et al. 2002), but we have an incomplete understanding of the ecological relationships that constitute this dependence.

In addition, the multi-species ecosystem approaches that have gained recognition in fisheries management during the past few years require more comprehensive exploration of the predator-prey interactions and habitat resources required by upper level fishes. The new emerging management paradigm focuses assessment and modeling efforts on identifying the role of physical environmental attributes, habitat, fishing impacts, and the biological community in the production of fish biomass (Department of Commerce 1997). An increased appreciation for the linkages between predatory fishes' year class strength and forage fish dynamics (Scharf et al., 2003) and the habitats upon which these forage species depend has resulted (Donovan et al., 1997; Stephenson, 1997). A greater knowledge of the roles that vegetated shallows play in the production of predatory fishes is of substantial value to fisheries management. This information is crucial in order to evaluate the effects that past coastal habitat modifications have had on fisheries' resource production and the design of subsequent management plans (Boesch and Turner, 1984).

The NMFS's "Fisheries Ecosystem Plan" specifically recommends that conceptual models of food webs be developed (NMFS 1999). These conceptual models can be combined to construct mechanistic models that will provide a useful tool capable of exploring various managerial approaches and predicting possible outcomes based upon system structure and its response to change. Problems and theories not easily addressed under field conditions can be examined. Model simulation provides an attractive alternative to resource managers because it allows for examination of methods that would be too expensive, difficult, or destructive to attempt in the real system (Hall and Day, 1977). Given the potential negative ecological and social consequences resulting from application of non-tested strategies models offer a valuable alternative.

As fisheries' management moves into the twenty-first century, armed with new techniques and technology, inclusion of previously overlooked and/or nonquantified parameters into assessment models is becoming possible. One of the greatest concerns and likely most important attributes affecting the marine ecosystems' production of important upper level resources is the alterations of its habitat composition. Littoral zones are highly productive at the secondary level the trophic level most relied upon by upper level fishes and these zones contain the habitats most often negatively impacted by human expansion (Odum, 1971). Significant habitat alterations can change the quantity and quality of production at lower trophic levels. Alterations in prey community structure in turn can affect the energetics of dependent upper level life forms. In order to understand the role each littoral habitat play in the production of upper level fishes and provide comparisons between habitats, spatially explicit models that quantify contributions in standard units must be constructed. Habitat specific spatial processes are particularly important in fisheries' models and will have implications for the design of marine reserves in coastal regions (Thorrold et al., 2001).

Summary of Objectives

1) Field Studies

(a) Describe monthly and annual species composition, biomass, number, and diversity.

(b) Determine sampling gear efficiencies and area swept in order to generate area estimates of biomass and number.

2) Laboratory Studies

(a) Describe and quantify trophic pathways and exchanges for striped bass, bluefish and weakfish.

(b) Determine dietary overlap of piscivores.

(c) Determine piscivore diets based on food web (pelagic or benthic) affinities.

3) Modeling Studies

(a) Construct bioenergetics models based on Hartman and Brandt's (1995b,c) physiology work to estimate growth based on daily consumption.

(b) Test model inputs for sensitivities.

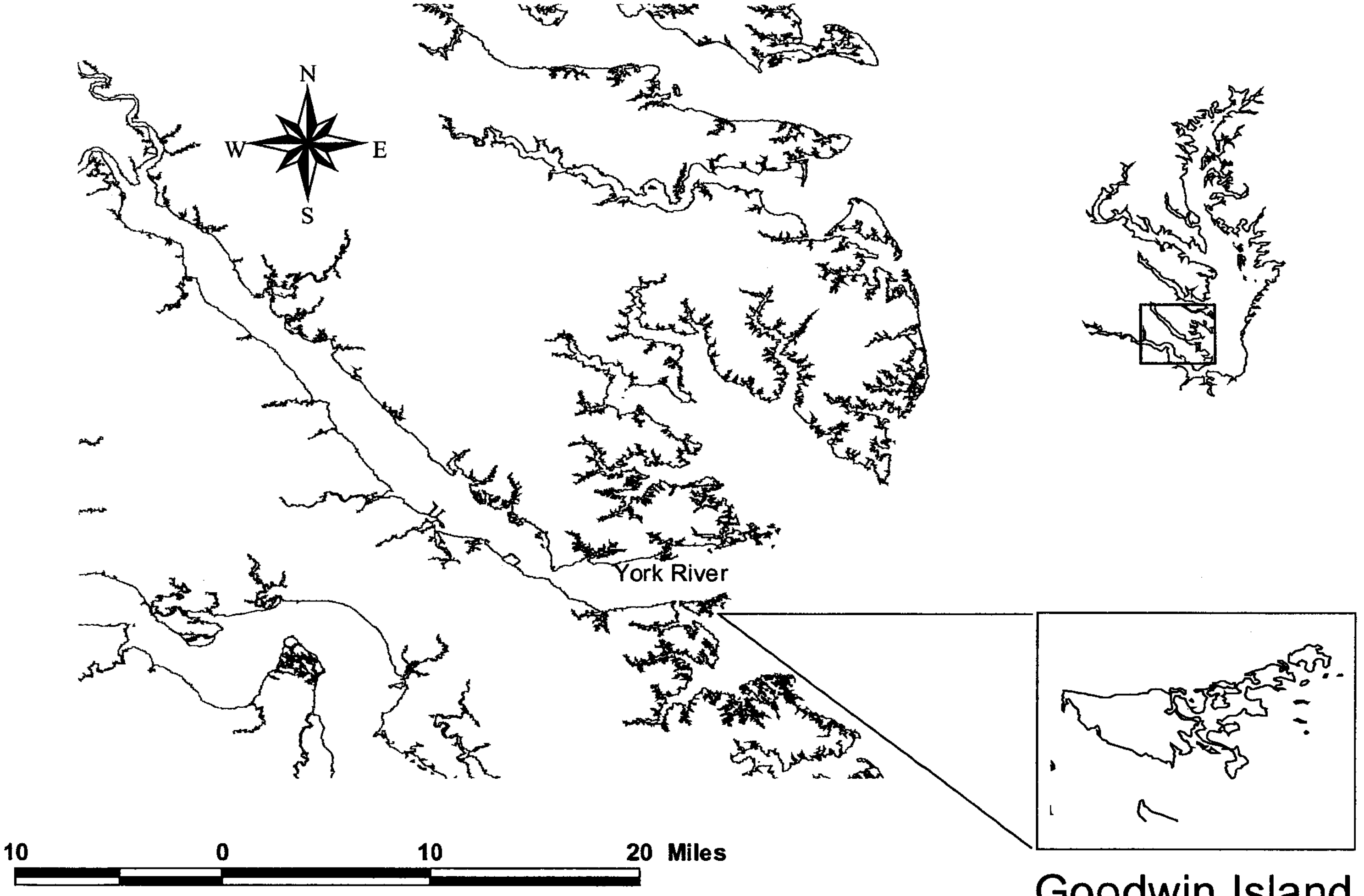
(c) Investigate growth advantages of seeking diel thermal sanctuaries in deep-water compared to shallow-water thermal structure.

STUDY SITE AND FIELD METHOD JUSTIFICATION

The Goodwin Island National Estuarine Research Reserve (GINERR) is located along the southern shore of the York River's mouth (Fig.1.1). It contains a littoral habitat diversity, which includes vegetated subtidal and intertidal zones that typify those traditionally found in mesohaline and polyhaline regions of the Chesapeake Bay (Buzzelli, 1996). GINERR provides an ideal littoral study site (defined as the area between the –2 m depth contour, relative to mean low water, and the high tide limit above the high marsh habitat) for several logistic and ecological reasons.

Considerable amounts of work covering various aspects of the site's lower level ecology have been conducted. Primary and secondary production and consumption have been estimated for the site and trophic pathways and transfers between lower levels determined (Buzzelli, 1996; Cicchetti, 1998 and Cicchetti and Hinchey, unpublished). When combined with this study's results, an ecosystem model can be formulated that will track energy from primary production through the various trophic levels until it is exported by transient predators or harvest by man.

Fig. 1.1. Study site at York River's mouth at entrance to Chesapeake Bay

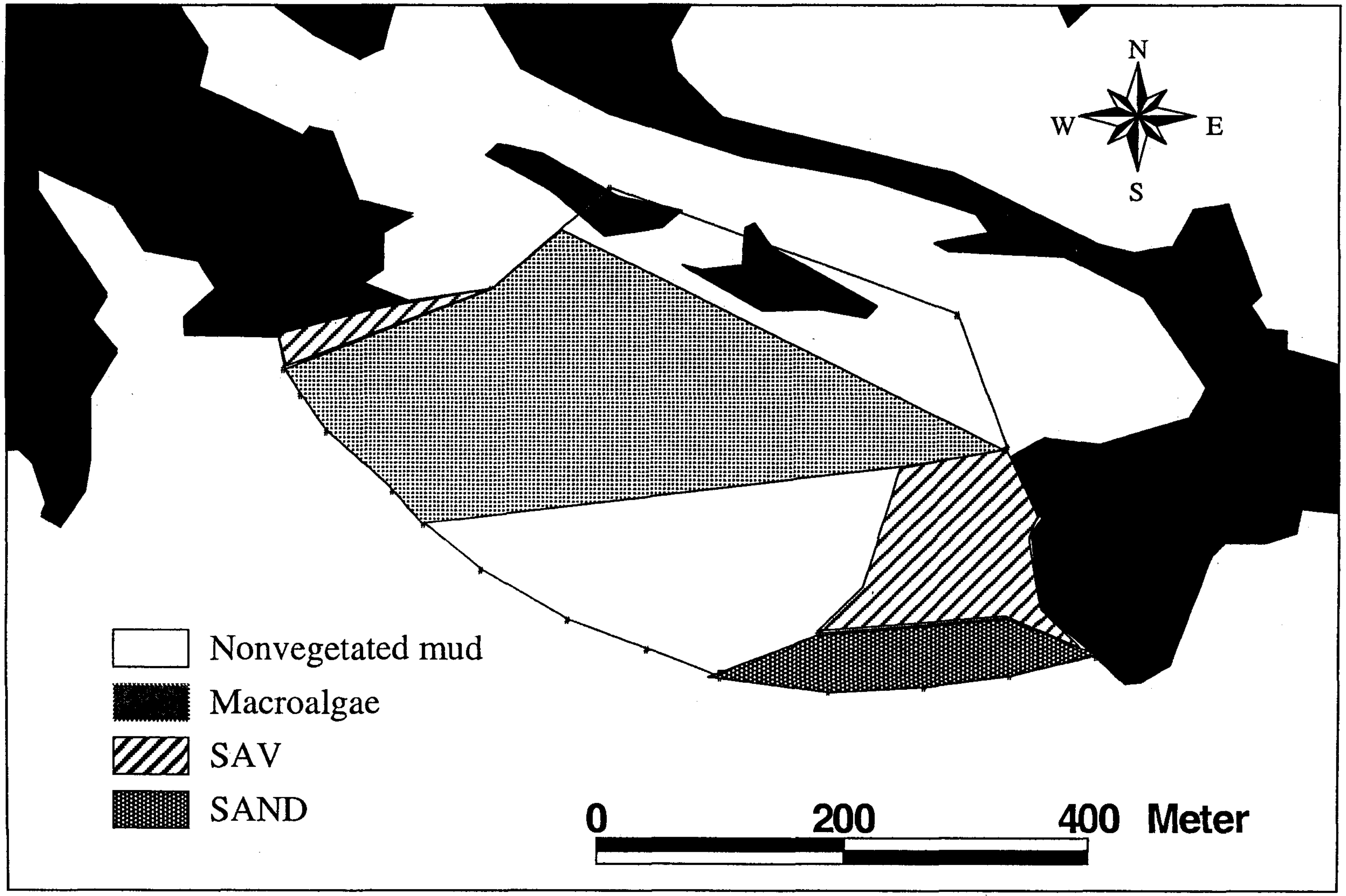


Goodwin Island's littoral zones consist of a mosaic of sand, seagrass *(Zostera* and *Ruppia*) meadow, mudflat, and marsh habitats, which most often overlap or are in close proximity to one another. Buzzelli's (1996) ecological surveys identified and quantified four littoral habitats: nonvegetated subtidal (-2.36m to –1.36m, 51.9%), vegetated subtidal (-1.36m to -0.36m, 18.5%), nonvegatated intertidal (-0.36m to 0.0m, 12.3%) and vegetated intertidal (0.0m to .36m, 11.1%). Examining subtidal habitats alone results in 74% nonvegetated and 26% vegetated.

In this study habitat composition and location were both important components in site selection. Composition was especially important because gear methods limited sample collection to a single location. In order for the selected site to typify the average vegetated Chesapeake Bay littoral zone it had to contain the appropriate habitat diversity and in relatively typical proportions. The site selected was surrounded by vegetated intertidal habitats on three sides. Coverage of intertidal habitats was not estimated because it varied greatly on tidal cycles. Based on a survey conducted in June of 2001 the subtidal portion of the site contained 5% sand, 10% seagrass meadow, 34% macroalgae, and 51% mud (Fig.1.2) or in simpler terms 56% nonvegetated and 44% vegetated.

Macroalgea is designated as a distinct habitat type in this work because extremely high densities of animals are routinely recorded among masses of drift algae (Tabb et al. 1962; Roessel and Zieman, 1970; Thorhaug and Roessler 1977; Gore et al. 1981, Sogard and Able, 1991) and it is one of the major proposed

Fig. 1.2. Haul-seine study site's benthic habitat composition.
All surrounding land was vegetated intertidal.



explanations for the often cited role of seagrass beds as nurseries (Thayer and Phillips, 1977). Given macroalgae's inclusion as a vegetated area the proportions of benthic habitats found in this survey were very similar to those found by Buzzeli for the whole island network, which characterized those found throughout the Bay's meso to polyhaline littoral habitats. Therefore, this study's site should provide representative samples of the fishes found in these habitats. Site location was important because it could indirectly bias the origin of gut content. A centrally located site surrounded by similar littoral habitats was selected in order to minimize the likelihood that fish stomach content was acquired in a habitat vastly different from that provided in study site.

One of the principle objectives of this study was to quantify the biomass, abundance, and assemblage structure of the ichthyofaunal communities occurring in a meso to polyhaline Chesapeake Bay littoral zone containing a typical composite of intertidal and subtidal shallow water habitats. Another no less important objective of this study was to identify and quantify stomach content of predatory fishes. Active gears like seines provided more accurate estimates of food consumption because they sample both low-activity non-foraging and actively feeding fishes (Hayward et al., 1989) and, in general, large-scaled sampling methods provide more accurate estimates of abundance, biomass, assemblage composition, and trophic consumption than small ones (Livingston, 1987). A fish's speed is proportional to its size (Blake, 1983; Webb and Weihs, 1983; Walters, 2002 pers. com. UBC, British Columbia, Canada); therefore, no single gear type can efficiently sample both slower smaller prey items and faster larger consumers. In order to collect fishes from across size classes that represented all of the trophic levels available and provide accurate estimates of all desired parameters two different appropriately scaled seines were used.

Temporal assemblage structure, species-specific abundance, and biomass across trophic levels were provided by concurrent operation of a small (prey) seine and a large haul-seine. Simultaneous collection of predator and prey provided the data necessary to examine parameters that influence predator and prey diversity and density. A commercial haul-seine was chosen as the large-scale sampling device for several reasons. This gear has historically provided large varied catches from the Bay's littoral zones and its size allows a very large area to be isolated relatively quickly, thus reducing gear avoidance. During operation the seine is swept across the entire enclosed area. This active and complete coverage augments its ability to estimate fish densities and establish assemblage diversity regardless of fish behavior. In addition a major step in incorporating multispecies or ecosystem approaches into fisheries management plans is the collection of gear specific statistics on catch, effort, and ecological impact of commercial gears. Haul-seine catches provided in this study will help establish these parameters.

CHAPTER 2. STRUCTURAL ANALYSIS OF ICTHYOFAUNA IN CHESAPEAKE BAY LITTORAL ZONE: DENSITY, BIOMASS, AND ASSEMBLAGE STRUCTURE DIVERSITY

ABSTRACT

Fifty-two different finfish species were captured in a typical meso to polyhaline Chesapeake Bay littoral zone from April to November in 2001. Collection methods involved two seines: one designed to sample smaller (prey) species and one commercial haul-seine designed to capture larger transient fish. A 30.5m prey seine sampled 352 m^2 and captured 32 finfish species. Ichthyofaunal diversity was greater but fish densities were similar to those determined by previous work in the same littoral zone using enclosure devices. Prey biomass peaked in early July at 9.74 g/m^{-2}, abundance followed in late July at 5.5 $/m^2$. Species diversity was greatest in September (n=20) due to presence of tropical and young-of-the-year (YOY) species. Commercially and recreationally important YOY included sheepshead (*Archosargus probatocephalus*), black drum *(Pogonias cromis*), northern puffer (*Sphoeriodes maculatus*), spadefish (*Chaetodipterus faber*), spot (*Leiostomus xanthurus*), red drum (*Sciaenops ocellatus*), spotted trout (*Cynoscion nebulosus*), striped bass (*Morone saxitilis*), winter flounder (*Pleuronectes americanus*), summer flounder (*Paralichthys dentatus*) and American eel (*Anguilla rostrata*). A 914m commercial haul-seine sampled 144,473 m^2 and captured 31 finfish species, including 17 that were not collected by the prey seine. Additional YOY species provided by this gear included sandbar sharks (*Carcharinus plumbeus*) and bluefish (*Pomatomus saltatrix*). Haul-seine catches were dominated by gizzard shad (*Dorosoma cepedianum*) in number

(30503) and biomass (18308kg), followed by Atlantic croaker (*Micropogonius undulatus*)(15825 and 6693kg), suggesting that these species may play a dominant role in the system's energy budget and nutrient export from the region. Striped bass, bluefish, and weakfish (*Cynoscion regalis*) were the dominant piscivores, exchanging prominence seasonally. Striped bass were most abundant and age distribution most diverse in spring (May) and early fall (Oct.). A complete absence was observed in late summer (Sept.). Bluefish were slightly more abundant in spring (May) but remained plentiful until early fall (Oct.). Weakfish abundance grew steadily until it peaked in late summer (Sept.). Marked decreases in bluefish and weakfish occurred in early fall (Oct.) with declining water temperatures and prey densities and rapid increases in striped bass density. Striped bass were the most abundant piscivore (1033) and contributed the largest biomass (593kg) followed by bluefish (312 and 137kg) and weakfish (303 and 105kg). Striped bass had the widest age distribution (0->11) followed by weakfish (1-8). Sampled bluefish (1-2) were predominantly age 1. All three piscivores showed a reduction in average size (age) during summer. Piscivore abundance and biomass was consistently greatest nocturnally. The dual seine gear approach supplied greater finfish diversity in a shorter period of time than trawl studies conducted in the area previously. Gear efficiencies for both seines were estimated using species and gear specific tag and recapture methodology and seasonal predator and prey densities determined. Significantly different gear efficiencies resulted due to tag location and water temperature alterations. Statistical analysis of repetitive runs of both gears indicated no significant efficiency differences within a species given identical tagging methods and similar water temperatures, but significant variation in recapture rates existed in both gears between species. Findings suggest that tagging methods can affect ability to measure gear efficiency, environmental temperature may have a significant effect on a mobile gear's efficiency, and seine gear may be inadequate to sample some species if they occur in low densities. Regression analysis of sampled ichthyofaunal diversities (prey seine vs. haul-seine) and prey seine density (abundance summed) verses individual piscivore densities (striped bass, bluefish, and weakfish) revealed no significant relationships.

INTRODUCTION

A disproportionately small effort has been devoted to coastal habitat evaluation, protection, and enhancement (Boesch and Turner, 1984). This approach has been due in part to the fact that single species management plans of the past ignored habitat diversity and species' interactions. Habitat differences in prey biomass and availability alter trophic energy intake and these differences in turn affect predator condition related to growth and reproduction (Lankford and Targett, 1994, 1997; Grecay, 1991; Grecay and Targett, 1996). Multi-species modeling approaches that are gaining increased support today in fishery science and management require a better understanding of such spatially explicit factors (Brandt et al. 1992).

Characteristically, estuaries are more nutrient rich and productive than either the sea or freshwater drainage that combined to create them. The most productive, and hence most important, part of an estuary is the intertidal and adjacent shallow water habitat (Odum, 1971; Pihl and Rosenberg, 1982; Weinstein, 1982). Commercial catch records indicate that the Chesapeake Bay's littoral zones once provided an astonishing abundance of upper level fishes (Hildebrand and Shroeder, 1928). Unfortunately, the Chesapeake and its adjoining bays of the Delmarva Peninsula have experienced a dramatic reduction in the coverage and distribution of highly productive littoral habitats. Submerged aquatic vegetation (SAV) a principle component to the zone's high productivity (Orth and Heck, 1980; Beck et al. 2001) has declined dramatically since 1930 (Orth and Moore, 1983, 1984). Loss has been due to disease (Cottam and Munro, 1954; Rasmussen, 1975), meteorological events (Orth et al., 2002), and declining water quality. The Chesapeake's water quality has been in decline since European colonization and the tobacco boom resulted in increased land clearance for agriculture that augmented sedimentation and burial of organic carbon. A gradual shift in the taxa responsible for primary production resulted, seagrass and benthic diatom pathways were reduced and the phytoplankton pathway was augmented (Jackson et al., 2001). Long-term environmental degradation, combined with overfishing and disease, has caused a decline in the resident oyster population as well (Hargis, 1999). This bivalve was once a keystone species in the Chesapeake that coupled benthic and pelagic production through its planktonic filtration and construction of three dimensional reef structures (Newell, 1988; Kennedy et al., 1996). Vertical reefs provided increased trophic resources and habitat for complex estuarine food webs including apex piscivores (Harding and Mann, 2001a,b, 2003). Salt marshes are also widely recognized as valuable nurseries for marine and estuarine fishes and crustaceans (Roundtree and Able, 1992; Knieb, 1997, Rozas and Minello, 1997; Beck et al. 2001) which are trophically important to transient piscivores (Roundtree and Able, 1992a; Hartman and Brandt, 1995a; Tupper and Able 2000; Walter and Austin, 2002; Walter et al. 2003), Unfortunately, the extent of salt marsh coverage by intertidal vegetation has also been reduced by extensive hardening of estuarine shorelines (Titus, 1998; Barnard et al. 2001). Prey consumption and trophic export from nonvegetated intertidal is less than that supplied by naturally depositional or erosional marsh edges (Cicchetti and Diaz, 2000), therefore, trophic export is negatively affected if hardening destroys natural salt marsh edge. If saltmarsh habitat remains but access to nekton is restricted, this can also have a detrimental effect on nekton production (Peterson and Turner, 1994; Hendon et al., 2000). Reducing prey production through habitat alterations may significantly reduce the amount of production that passes through predator–prey interactions and thus directly affect the growth and abundance of transient piscivores (Knieb, 1997; Tupper and Able, 2000). Fisheries managers now recognize the importance of habitat to the productivity of fish stocks (Rubec et al. 1998, Friel, 2000). Successful piscivore restoration efforts will likely require a much more thorough understanding of the utilization of highly productive littoral habitats by both predator and prey.

Alterations induced by climate and man can often cloud energetic links between declining production and habitat modification (Boesch and Turner, 1984). Numerous investigators have stressed the critical importance of littoral zones and the intertidal and submerged habitats they contain as nurseries and feeding grounds to marine fishes and invertebrates (Gunter, 1956, 1961; Nixon and Oviatt, 1973; Subrahmanyam and Drake, 1975; Daibner, 1977; Weinstein, 1979; Boesch and Turner, 1984; Currin et al., 1984; Thayer et al. 1984; Roundtree and Able, 1992a; Costanza et al. 1997; Heck et al. 1997, Knieb, 1997; Able and Fahay, 1998; Dionne et al. 1999; Tupper and Able, 2000; Beck et al. 2001, Stunz et al. 2002; Nemerson and Able, 2003) and emphasized the need to further investigate these contributions

(Nixon and Oviatt, 1973; Subrahmanyam and Drake, 1975; Bozeman and Dean, 1980; Currin et al., 1984; Weinstein et al., 1984; Knieb,1997; Beck et al. 2001). Littoral habitats are known to produce large quantities of suitable prey items for both juvenile and adult piscivores but functional linkages between prey supply and predator demand and their dependence on habitat have not yet been quantitatively defined (Brandt et al., 1992).

The mosaic of habitats including SAV, intertidal salt marshes, subtidal marsh creeks, macroalgal mats, and nonvegetated sand and mud flats that make up the typical Chesapeake Bay littoral zone are extremely productive and support a large diverse nekton populations. The importance of SAV habitats with regard to crustacean prey species is well documented (Edgar and Shaw, 1995a; Howard et al., 1989; Edgar et al., 1994). Crustacean reliance can be so pronounced that their biomass is positively correlated with that of the vegetation (Howard et al., 1989; Edgar et al., 1994). Fish assemblages around these grasses can be twice as high as surrounding nonvegetated bottom (Edgar and Shaw, 1995a). Trophic investigations around SAV have revealed that crustaceans can be a significant portion of transient fishes' diets (Lascara, 1991; Edgar and Shaw, 1995c). Not surprisingly, fish production in some of these grassbeds is highly correlated with seagrass biomass and its associated crustacean production (Edgar and Shaw, 1995b). Submerged aquatic grasses are by no means the only beneficial littoral habitats. Many investigators have stressed the importance of salt marshes as nurseries for crustaceans and juvenile fishes (Gunter, 1956, 1961; Nixon and Oviatt, 1973; Subrahmanyam and Drake, 1975; Daibner, 1977; Weinstein, 1979; Boesch and Turner, 1984; Currin et al., 1984, Rountree and Able, 1992; Knieb, 1997). Dietary analysis of striped bass sampled from around this habitat type revealed that crustaceans are also a major component of energetic exchange (Tupper and Able, 2000). A high diversity of prey species with wide geographic distributions is found in marsh creeks (Weinstein, 1979; Weinstein et al. 1980; Smith et al. 1984; Roundtree and Able, 1992a). Some investigators (Weinstein and Brooks, 1983; Sogard and Able, 1991) have found that the density of fishes found in marsh creeks can exceed that sampled in *Zostera* beds. Surprisingly, direct comparisons between macroalgae and *Zostera* provided similar densities of decapods. *Zostera* did, however, provide higher densities of fishes. Both vegetations (*Zostera* and macroalgae) provided improved densities (both fish and decapod) compared to unvegetated bottoms (Sogard and Able, 1991). While fish densities in vegetation do not always exceed those found over immediately adjacent bare substrate (Ferrel and Bell, 1991), the increased structure provided in vegetation seems to have a positive effect on species diversity and density (Orth and Heck, 1980; Orth, Heck and Van Montfrans, 1984; Heck et al. 1989; Edgar and Shaw, 1995a,b; Wyda et al. 2002). Though the lower levels of may littoral habitats have been well studied and provided increased evidence of high piscivore prey productivity and availability in these zones, little is know about how these resources benefit transient upper level fishes.

Predator demand and prey supply define the supply demand relationship that regulates piscivore production (Ney, 1990). Recent work by Hartman and Brandt

(1995d) suggests that the Chesapeake's striped bass, bluefish, and weakfish production in the oligohaline portion of the Bay is currently being limited by prey supply. Plant diversity within a community strongly influences the magnitude and variance of ecosystem processes (Tilman, 1999). Loss of energy and refuge providing vegetated littoral habitats, essential to the Chesapeake's production of infaunal and epifaunal invertebrate biomass, may have limited crustacean and forage fish prey supply and increased prey accessibility of both forage species and juvenile piscivores. The potential impact of limiting trophic resource is obvious. The effects of refuge decimation on forage species and juvenile piscivores are not as clear; but severe depletion of either due to predation will potentially result in lower fishery yields (Boesch and Turner, 1984). Clearly, more needs to be learned about the role these zones play in the production of such fishes (Knieb, 1997).

Previous littoral studies have focused on lower trophic levels (Teal, 1962; Carr and Adams, 1973; Cicchetti, 1998; Minello and Rozas, 2002) and/or on a specific microhabitat such as a shallow sub-tidal embayment (Nixon and Oviatt, 1973; Ayers, 1995), sub-tidal creek (Weinstein and Walters, 1981; Ryer, 1987; Roundtree and Able, 1992a), eelgrass meadows, (Heck and Orth, 1980, Orth and Heck, 1980; Ryer, 1987; Stunz et al. 2002), macroalgea (Wilson et al., 1990), oyster reefs (Harding and Mann, 1999, 2001, 2003) or salt marsh edge (Peterson and Turner, 1994; Tupper and Able, 2000; Stunz et al. 2002). Though these studies have established high production of potential prey species within microhabitats commonly found in littoral zones they have not considered the whole community or its trophic linkage to transient consumers (Mattila, 1992).

The typical Chesapeake littoral zone consists of many varied habitats that overlap or are in close proximity to one another (Cicchetti, 1998). Generally swimming speed increases with fish size (Blake, 1983; Webb and Weihs, 1983). Due to this size/speed relationship, small fishes tend to remain in microhabitats near or in protective cover while larger fishes move between and/or through such habitats in search of prey (Harrel and Dibble, 2001;Walters, 2002 pers. com., UBC, British Columbia, Canada). Though seagrass habitats are believed to have a positive effect on icthyofaunal species richness and production (Howard et al., 1989; Edgar et al. 1994), fish densities within seagrass beds are not always higher than those found above the bare substrata immediately adjacent to vegetation (Ferrel and Bell, 1991). Crustacean density and that of subaquatic grasses are tightly correlated (Howard et al., 1989; Edgar et al., 1994). The close proximity of vastly different microhabitats with unevenly distributed prey items and the inherent speed of larger fish increases the likelihood that piscivores are transitioning between various habitat types opportunistically benefiting from available prey. A state of constant flux makes determination of exact location of predation difficult. This study used a large-scale method of sampling larger fishes that was capable of including all the various littoral habitats that may contribute to the production of predatory fishes. A dual gear approach also provided for congruent sampling of available prey communities.

Enclosure devices are generally recommended for quantification of small nekton species (Rozas and Minello, 1997) but these generally small scale approaches are ill suited to estimating densities of large fish (Jacobsen and Kushlan, 1987; Cicchetti, 1998). Seines are commonly used to sample large fishes but the gear can have variable catch efficiencies due to environmental conditions and typically has very different species-specific efficiencies (Weinstein and Davis, 1980, Allen et al. 1992). Low catch efficiencies commonly associated with seines can be corrected for, if efficiencies can be made more precise through standardizing gear methodology, sample site, and harvest methods.

Two very different seines were chosen to quantify the entire icthyofaunal community temporally. Each was designed to collect fishes of different sizes and thus expand the size distribution sampled. A small seine (30.5m) with a reduced mesh (.75mm) targeted smaller specimens including young-of-the-year piscivores and forage species. The efficiency of standard sampling methods varies greatly in time and space; therefore, efficiency should be estimated at least once a season (Allen et al. 1992). The small-scale seine provided a means of repetitively sampling recapture rates of various fishes under different conditions, a characteristic necessary to estimate species-specific gear efficiency and examine the various factors that affect it temporally.

This small seine was not adequate to sample piscivores for several reasons. Its reduced mesh made it too slow to trap larger/faster fishes. Its small size also prevented it from being used as an enclosure device. Reduced size also prevented simultaneous inclusion of various littoral habitat habitats. A large haul-seine (914m long, 3.04m tall and 7.62 containing mesh) was employed in order to isolate the larger icthyofaunal community within an area large enough to include various littoral habitats. The net's length allowed it to be stretched from one point of land to another thus isolating a large area of littoral zone. In this manner the haul-seine was used as a giant enclosure device in order to minimize gear avoidance. Sampling a larger area augmented catches diversity and provided more representative estimates of abundance, biomass, and assemblage composition of larger fishes (Livingston, 1987). In addition, commercial gear use provided fishery independent determination of catch composition, effort (catch per area), and gear related habitat alteration estimates valuable to managers but difficult to obtain from commercial reports. Establishing specific statistics on commercial gears is especially important to incorporating multispecies and ecosystem approaches into fisheries management plans for multi-species fisheries like the Chesapeake's. True catch composition including bycatch and the unique ecological consequences of each gear's operation must be included in ecosystem models if they are to realistically describe the interacting factors driving subsequent fishery yields and to provide for improved management strategies based on model predictions.

Modeling is a tremendous asset to fishery science but improving our knowledge of ecological function through extensive field and laboratory efforts can strengthen its contributions. Increasing our understanding of habitat specific ecological function requires field research within each unique habitat. This study is the first step in quantifying the importance of littoral habitats to transient fishes. It provides a temporal account of the environmental variables, assemblage structure, biomass, abundance, and density of predator and prey in a meso to polyhaline littoral zones containing a typical diversity of submerged and intertidal habitats. Such parameters are necessary for the construction of multi-species interaction models capable of quantifying the factors influencing energetic exchanges and thus providing for better management at various trophic levels.

The specific objectives of the study are to: determine species-specific gear efficiencies; determine icthyofaunal assemblage, abundance, biomass, and density temporally; statistically examine diel differences in piscivore catch; use a Margalef's diversity index to compare samples; examine relationship between predator and prey densities; discuss bycatch and ecological impact of haul-seine fishery.

The study was intended to improve information on the role that littoral habitats serve with regard to various ecologically and economically important finfish species. Establishing a fish's density is the first step in establishing scale-dependent linkages between biological function and the biological and physical structures that regulate a habitat's contributions to that stock. Densities provide a means of comparing biological function between habitats based on species' abundances (FWS, 1980a, 1980b, 1981; Terrel and Carpenter, 1997) that allow habitats to be identified and preserved based on their contributions as "essential fish habitats" (EFH), however, densities alone do not provide for definite determination or categorization of EFH. Future works must show that a given habitat not only contains a greater density of fish but also explicitly provides better fitness (growth or energetic savings).

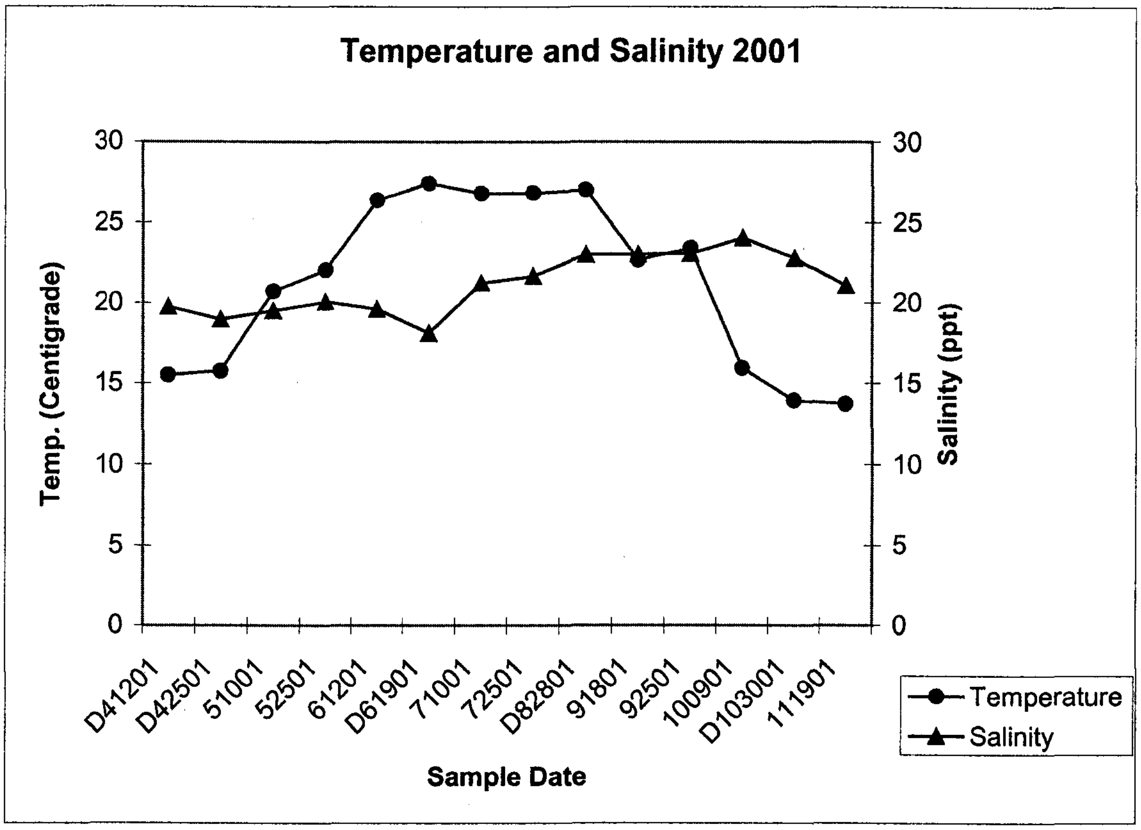
STUDY SITE AND METHODS

Study site

The Goodwin Island National Estuarine Research Reserve (GINERR) is located along the southern shore of the York River's mouth (Fig.1.1). Its littoral zone (defined as the area between the –2 m depth contour, relative to mean low water, and the high tide limit above the high marsh habitat) includes vegetated subtidal and intertidal habitats and physical characteristics (Fig. 2.1) and temperature and salinity regimes that typify those traditionally found in mesohaline and polyhaline littoral regions of the Chesapeake Bay (Buzzelli, 1996).

In June of 2001, the subtidal portion of the study site contained 5% sand, 10% seagrass meadow (*Zostera and Ruppia*), 34% macroalgae mats (primarily *Ulva lactuca* and *Gracilaria foliifera*), and 51% mud (Fig.1.2), or in simpler terms, 56% nonvegatated and 44% vegetated. The site was surrounded by vegetated (*Spartina* dominant) intertidal habitats on three sides. Coverage of intertidal habitats was not estimated because it varied greatly on tidal cycles. Macroalgae was designated as a distinct habitat type in this work because extremely high densities of animals are routinely recorded among masses of drift algae in seagrass beds (Tabb et al. 1962;

Figure 2.1: The temperature (C°) and salinity (ppt) during each sample are given below. Daylight samples are marked with a D preceding date.



Roessel and Zieman, 1970; Thorhaug and Roessler 1977; Gore et al. 1981) and it is one of the major proposed explanations for the often cited role of seagrass beds as nurseries (Thayer and Phillips, 1977). More recent work suggests that macroalgea offers juvenile blue crabs better predation cover than eelgrass (Wilson et al., 1990) this habitat may, therefore, play a much larger role in predator prey dynamics than previously suspected. Given inclusion of macroalgae as a vegetated area, proportions are very similar to those found by Buzzeli (1996) for the whole Goodwin Island network, which he concluded contained habitat proportions typical of most meso to polyhaline Chesapeake Bay littoral zones; therefore, the study site selected should provide representative samples.

Sampling periodicity

Haul-seine sampling began in May of 2000 and continued until November. Samples were collected during day and night. This year's fieldwork was used as a pilot study to establish sampling protocol, improve precision of gear operation techniques, and learn about fishery's market. Distinct diel differences in catch were observed in 2000 but not statistically examined. The dual gear samples reported in this study started in April and continued through November in 2001. Samples were collected twice monthly, except for November when only one sample was collected. One haul-seine sample (August, nocturnal) and one prey seine sample (June 19th) were not reported due to gear failure.

Daylight haul-seine samples were collected every other month throughout the study period to provide for statistical comparisons of diel catch differences of piscivores. Prey seine samples were conducted during the day and at mid-tide for ease of operation, to provide for suitable landing areas, and to sample species that spread out over marsh on high nocturnal tides.

Methods

A small-scale prey seine 30.5m long and 3m tall consisting of 0.75 cm stretched mesh was used to collect smaller species. Twelve prey seine samples were collected from April to November 2001. All trials were conducted during daylight hours at mid-tide in conjunction with haul-seine operations. The seine was run at mid-tide because this period provided suitable landing areas (Cicchetti, 2000 pers. Com., EPA ; Buckel and Conover, 1997; Austin, 2000 personal communication). Samples were collected from an area within the sweep of the larger seine during daylight hours.

The purpose of small (prey) seine collections was twofold. First, it provided temporal assessment of smaller nekton and YOY assemblage structure, species-specific abundance, and biomass; these smaller forage species and juveniles would be potential prey items for larger predatory fish. Second, the small scale of this gear made determination and examination of factors affecting gear efficiency easier.

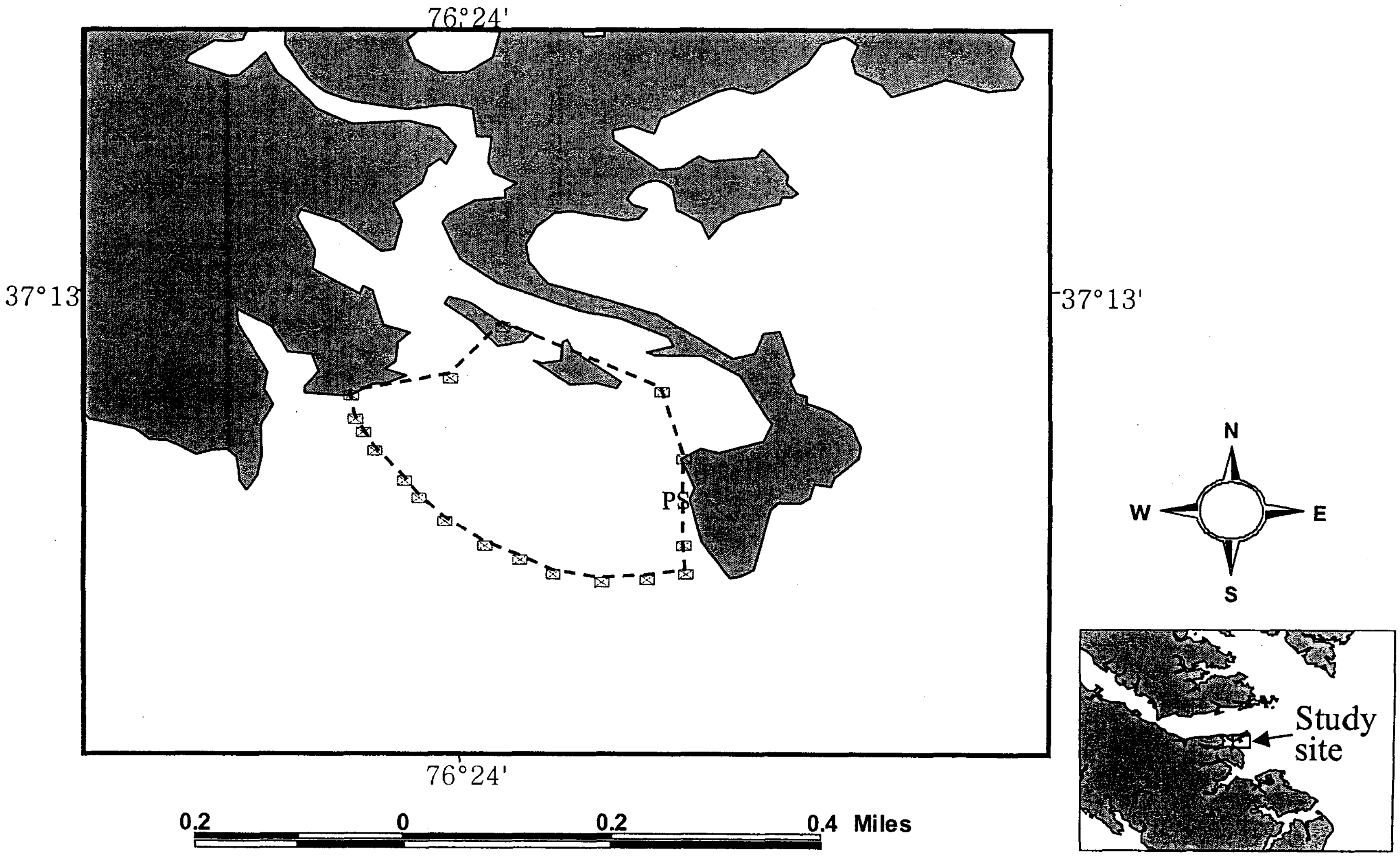
To determine the area sampled by the small seine the net was deployed from shore and the outside border of the net's sweep marked with poles as the net pulled through the water. The seine was operated in the same manner and location as during the study. The distance and angles to marker poles was subsequently measured and the results graphed. Area swept was determined by measuring the distance and angles to marker poles and simple geometry. This operation was not replicated because previous experience with gear indicated that factors such as tide and wind have such a large effect that defining deviations in an area under identical environmental conditions would not provide any increased accuracy in estimating true area covered during individual field samples.

The prey seine sampled 352 m^2 when deployed at a 90-degree angle to shore and pulled in an arch directly back to shore. Resistance put a curve in the net that could not be avoided which covered 58.25 m^2. If prey species are assumed to be actively fleeing the area within the bulge due to the net's deployment as Pihl and Rosenburg's (1982) suggest may occur under clear water no wind conditions then undisturbed sampled area would be 293.75 m^2. The total area of 352 m^2 was used to calculate prey densities in this study because it provided more conservative prey density estimates.

The haul-seine used in this study adhered to the regulations governing haul-seine gear as set forth in the Laws of Virginia Relating to Marine Resources of the Commonwealth (1998), which allowed for comparisons between this study's gear impacts and catches and those of commercial operations. The net consisted of ten separate sections that when tied together (lapped) created a single seine 914m (3000 ft) long. All sections were 3.04m (10 ft) tall with floats along the topline and leads along the bottom. The first 762m (2500 ft) of this seine consisted of five sections composed of 7.62cm (3 in) mesh. The last two shorter seines contained a reduced mesh of 5.08cm (2 in) in order to decrease gilling during the landing procedure. Catch was gradually forced into a small area by systematically pulling each section to shore and then removing it. Eventually, the catch was contained within a small circle created by the landing wings. A box containing a bottom (pocket) would then be tied between the terminal ends of the wings and a heavily weighted seine, called a wing, pulled across the area within the circle forcing the catch into the pocket. The haul-seine was always deployed at high tide in a method that prevented escape to deep water. The tide was allowed to drop and the net fished on the subsequent low tide.

The area swept by the haul-seine was determined with a hand held geographical positioning system (GPS) and Arcview © software. On the net's first deployment, the net was marked at each terminal end and every 30 meters. Consecutive net operations followed these marks. Latitude and longitude of marks were subsequently entered into an Arcview © program in order to determine area within gear. The haul-seine enclosed and sampled 144,473 m^2 or 35.7acres (Fig. 2.2). This is an extremely large sample area but it was necessary to enclose enough area to provide good estimates for large, fast moving fishes.

Fig. 2.2. Area of haul-seine site is marked with dashed line. Prey seine site which contained seagrass, mud and sand is marked with PS.



All fish collected in the prey seine were retained. Haul-seine catches were often too large to allow for total retention. Large species-specific catches were measured by volume methods. Bushel baskets would be filled and counted and unneeded fish released quickly to promote survival. The number of fish of a given species in three different baskets was counted and the average used to estimate total abundance. If species' number exceeded one hundred and fifty, only fifty specimens were randomly chosen and retained. Harvested specimens were placed in ice aboard vessels to deter deterioration. Retained fishes and crustaceans were transported to the lab and worked up within twenty-four hours.

Laboratory methods

Laboratory processing included measuring fish length (+ or – 1.0mm total length, TL) and weight (+ or – 0.1g wet weight after blotting). Measurements were used to create length weight regressions and to determine average biomass so that total catch biomass could be back calculated when volume measurements of abundance were necessary.

Total length to wet weight regressions were determined for species occurring in large enough numbers. Blue crab regressions reconstruct wet weight based on carapace width. Regressions were used to estimate weight of any specimens for which live weight could not be determined.

Gear Analysis

Gear efficiency

The mark recapture approach to gear efficiency estimation was duplicated for both seines. Tagging methods varied due to size restrictions imposed by fish. Prey seine fish were fin clipped and large fishes captured in the haul-seine were tagged with a T bar tag. Water temperatures were measured with a handheld thermometer for prey seine trials and through remote sensing equipment (GINERRS) for haul-seine work. Tagged fishes were released at a central location within the both nets' sweep after the gear was deployed as described in field methods. Gears were then swept across the bottom in a normal fashion, tagged fishes captured, and counted.

Various species were used to assess prey seine gear efficiency, including mummichog (53-83mmTL), striped killifish (49-90mmTL), sheepshead minnow (49-58TL), Atlantic silverside (65-100mmTL), red drum (43-72mmTL), spotted trout (110-163mmTL), and blue crab (25-75mmTT). Three trials consisting of a pair of tests were conducted. The first and second trial sets were carried out on November 6 and 7th (13 C°). Fishes were marked with caudal clips in the first trial of each day followed by dorsal clips. Clipping the tip of the swimmer fin marked blue crabs. The third trial set was conducted on December 1st (9C°) and both groups consisted solely of mummichog. Each groups was marked dorsally but in a unique manner. Striped killifish, Atlantic silverside, red drum, spotted trout, and blue crab were not included in this trial or statistically examined because availability resulted in low sample numbers and in some cases handling and marking stress resulted in questionable recapture rates. Mummichog were suitable for more stringent analysis because they were abundant and resilient to stress. Six hundred and sixty-five mummichog were marked in all (Appendix 1, Tables 1and 2).

Summer flounder, Atlantic croaker, spot, pinfish, red drum, black drum and gizzard shad recapture rates were examined in the haul-seine (Appendix 3 contains size distributions of tagged and recaptured fish). All fishes were tagged with a T-bar tag behind the dorsal fin. Efficiency studies were conducted in June (22C°) and October (20C°). Croaker was chosen for statistical analysis because they were consistently available and tolerated experimental methods well. Unfortunately, the only large piscivore tagged was red drum. No weakfish, bluefish, or striped bass were tagged. Weakfish and bluefish are metabolically ill suited and the transient nature of striped bass made their use problematic. A November trial was attempted to capture striped bass for mark recapture but gear failure prevented completion.

Statistical analysis of prey seine efficiencies

Chi-square analysis was used to compare the ratios of recaptured fish labeled in the same manner in order to examine the effect of tagging method on efficiency. This statistical method was also used to compare the odds of recapture of similarly marked fish at different water temperatures to determine if this environmental variable significantly altered gear's efficiency. The odds of each recapture rate's occurrence between trials were also compared using chi-square.

Catch Analysis

In addition to determining species-specific abundance, biomass, and density for each sample the size structure of the six most abundant (annual) species for each gear will be analyzed. Age structure of striped bass, bluefish, and weakfish will be estimated based on length at age regressions (Robillard et al., in prep.; Bobko et al., in prep; Bobko et al. in prep.).

Diversity

A Margalef's species diversity index (1958):

1) Index = (# species −1)/(log (# total sample size)

was formulated for both gears' catches monthly, in order to compare diversity over time. Regressions were used to determine if water temperature and gear diversity were related. Diversity indices were then analyzed to determine if prey diversity was significantly related to haul-seine diversity.

Diel differences

The logistics of setting up, mending, and operating a gear as large as the haul-seine used in this study, made replicate hauls almost impossible. Operations were conducted twice a month from April to November. Daytime hauls were conducted once every other month throughout the study period to provide for diel catch comparisons.

Within species, abundance data were summed across daytime and closest occurring nocturnal haul-seine dates. Totals were compared to determine if diel differences in haul-seine catches of striped bass, bluefish, and weakfish were significant. Even odds of abundance were assumed between day and night. Statistical likelihood of results and these odds were then compared through Chi-square analysis.

Predator-prey density correlations

The correlations between predator (striped bass, bluefish and weakfish) and prey densities (abundance) were examined through regression analysis. Prey densities were summed and this sum compared to striped bass, bluefish, and weakfish densities to determine if significant relationships existed. It was hypothesized that a correlation between the two may exist if greater prey densities motive predator immigration resulting in increased piscivore densities.

RESULTS

Gear efficiency

Percent recaptured for dorsally clipped mummichog ranged from 41-46% and caudally clipped fish from 60-61% on consecutive days (Nov. 6 and 7). The average size of dorsally clipped mummichog on Nov. 7 was 66 mm TL the average size of recaptured fish was 64 mm TL. On the third trial date (Dec. 9) all fish were dorsally clipped and percentage recaptured ranged from 79-80%. Chi-square analysis indicated that no significant difference in recapture existed between trials when fish were clipped in the same location at the same water temperature ($p=0.48$ dorsally clipped Nov., $p=0.85$ caudally clipped Nov., and $p=0.81$ dorsally clipped Dec.). Significant differences in the odds of recapture resulted due to tag location ($p=0.001$, Nov. dates dorsal vs. caudal). Chi-square analysis also indicated that a significant difference ($p=0.0001$, Nov. dorsal vs. Dec. dorsal) in the odds of recapture resulted between identically tagged fish at different water temperatures (Nov. 13C° vs. Dec. 9C°).

Prey seine recapture rates of other finfish ranged from 43-100%. Percentages should be viewed with some skepticism due to the small sample sizes (2-38) and/or low tolerances to handling stresses; a notable problem with Atlantic silverside.

Average finfish recapture rate across species (Nov. 6 and 7 only) was 57%. Blue crab (n=16) had a low recapture rate, likely due to active seine avoidance and terrestrial escape. Recapture rates and standard deviations are presented in (Fig. 2.3).

Sample sizes for most finfish species examined during the haul-seine gear efficiency test were small. Summer flounder and black drum (n=4 and 2) sample sizes were so small that findings provide little more than antidotal information. Four out of seven red drum tagged were recaptured. Gizzard shad, spot, and pinfish numbers equaled or exceeded thirty. Species specific recapture rates and the mean percent retention across all species examined (50%) is presented in Figure 2.4.

The haul-seine's large size and associated operational efforts prohibited a large number of haul-seine efficiency trials. Only two trials were performed. The first occurred on June 3 (22 C°) and the second on October 6 (20C°). In all 189 croaker were tagged, 49.7% were recaptured in June and 50% were recaptured in October. Chi-square analysis of the two indicated (p=0.98) no statistical difference in the net's recapture rate. (For more specific information on gear efficiency works look to Appendix one tables 1-3.)

Catch

Species assemblage structure and size varied between gears seasonally and annually. The reduced mesh of the prey seine consistently retained much smaller

Fig. 2.3. Prey seine gear efficiency estimates for all species examined including blue crab and an average finfish recapture rate. All species and average based on November samples only.

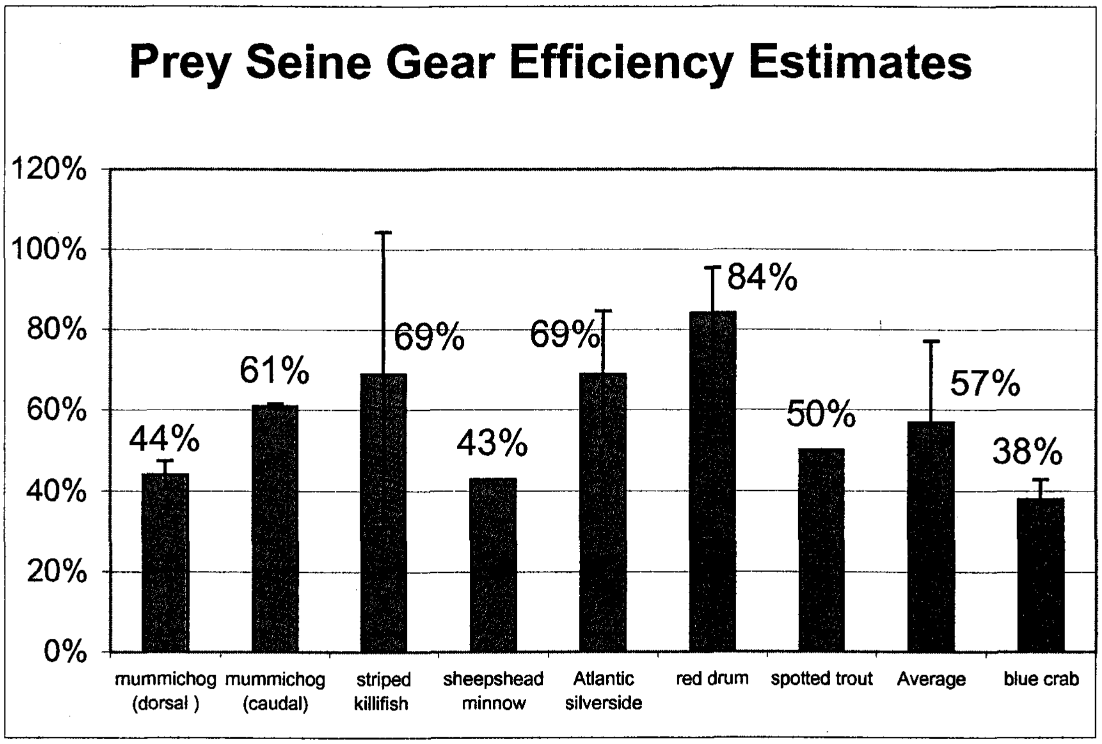
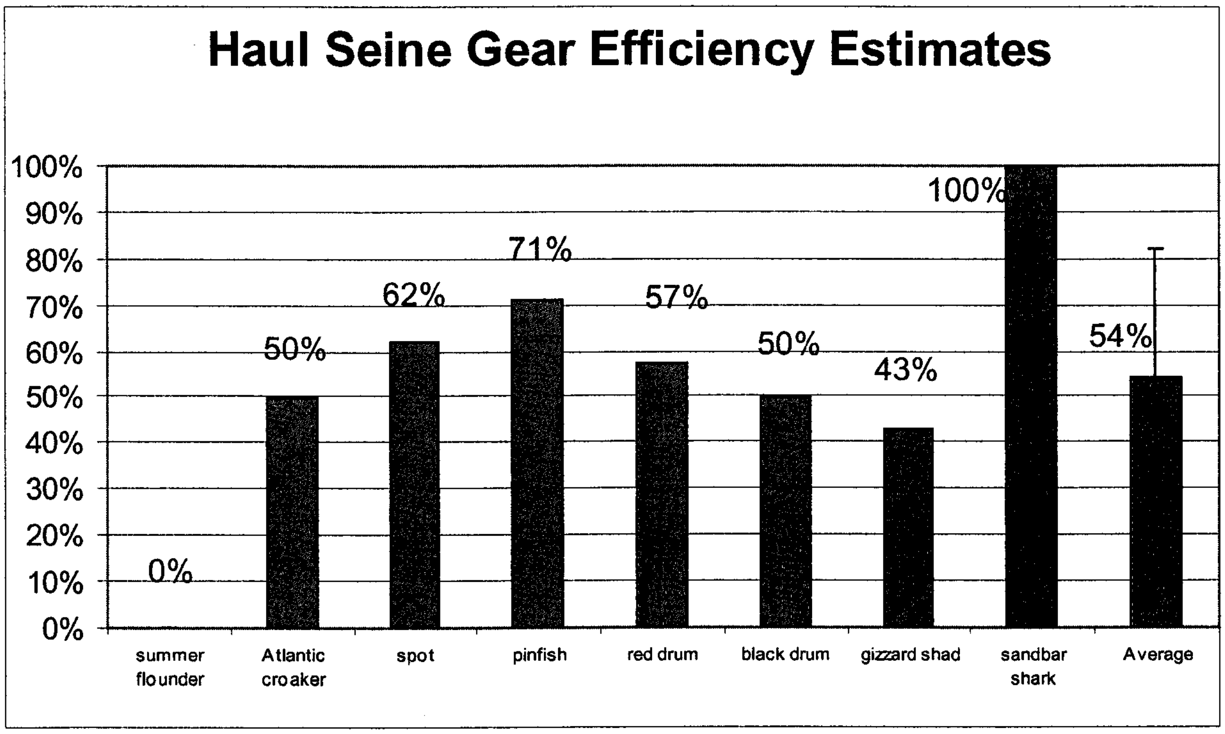


Fig 2.4. Haul-seine recapture rates including average across species.



fishes, which included forage species and YOY, than the haul-seine. Several species of YOY were collected in both gears. YOY sandbar sharks, cownose rays, and bluefish were captured in the haul-seine only. Gear bias in the case of these YOY may suggest that the young of these species did not occur in high enough densities, were too large, and/or mobile to be collected in the slower smaller prey seine (Table 2.1).

Prey Seine

The prey seine samples contained 33 species, 17 of which occurred in large enough numbers to produce meaningful length (mm) wet weight (gm) regressions (Table 2.2). Prey seine catches varied in assemblage structure seasonally (Table 2.3) due to alterations in species-specific abundance and biomass. Graphs of seasonal abundance and biomass for the ten most abundant species captured in the prey seine can be found in Appendix 2. Size distributions for the six most abundant species can be found in Appendix 3.

The largest number of species (20) was sampled in mid-September, when sub-tropical species and YOY contributed to the catch. Augmentation in diversity due to these species resulted in the highest Margalefs diversity index recorded. The smallest number of species (6) was collected in April when the lowest water temperatures of the study occurred. Statistical analysis of prey diversity's dependence on temperature revealed that no significant relationship existed between the two (Fig 2.5, Appendix

Table 2.1. The table is meant to be a reference for species identification and gear of capture. It lists species captured in prey seine then haul-seine. Both are listed in order of relative abundance.

Common name	Scientific name	Gear of capture
Blue crab	*Callinectes sapidus*	prey seine
Atlantic silverside	*Menidia menidia*	prey seine
Silver perch	*Bairdiella chrysoura*	both
Bay anchovy	*Anchoa mitchilli*	prey seine
Mummichog	*Fundulus heteroclitus*	prey seine
Striped killifish	*Fundulus majalis*	prey seine
Rainwater killifish	*Lucania parva*	prey seine
Naked goby	*Gobiosoma bosc*	prey seine
Spot	*Leiostomus xanthurus*	both
Northern pipefish	*Syngnathus fuscus*	prey seine
Oyster toadfish	*Opsanus tau*	both
Skilletfish	*Gobiesox strumosus*	prey seine
Red drum	*Sciaenops ocellatus*	both
Fourspined stickleback	*Apeltes quadracus*	prey seine
Striped blenny	*Chasmodes bosquianus*	prey seine
Spotted trout	*Cynoscion nebulosus*	both
Dusky pipefish	*Syngnathus floridae*	prey seine
Summer flounder	*Paralichthys dentatus*	both
American eel	*Anguilla rostrata*	prey seine
Striped mullet	*Mugil cephalus*	both
Atlantic thread herring	*Opisthonema oglinum*	both
Striped bass	*Morone saxatilis*	both
Feather blenny	*Hypsoblennius hentz*	prey seine
Halfbeak	*Hyporhamphus meeki*	prey seine
Atlantic needlefish	*Strongylura marina*	prey seine
Black drum	*Pogonias cromis*	both
Northern puffer	*Sphoeriodes maculatus*	both
Spadefish	*Chaetodipterus faber*	both
Winter flounder	*Pleuronectes americanus*	prey seine
Chain pipefish	*Syngnathus louisianae*	prey seine
Hogchoker	*Trinectes maculatus*	prey seine
Striped anchovy	*Anchoa hepsetus*	prey seine
Sheepshead	*Archosargus probatocephalus*	prey seine
Gizzard shad	*Dorosoma cepedianum*	haul-seine
Croaker	*Micropogonias undulatus*	haul-seine
Spot	*Leiostomus xanthurus*	both
Striped bass	*Morone saxatilis*	both
Bluefish	*Pomatomus saltatrix*	haul-seine
Weakfish	*Cynoscion regalis*	haul-seine

Silver perch	*Bairdiella chrysoura*	both
Summer flounder	*Paralichthys dentatus*	both
Hickory shad	*Alosa mediocris*	haul-seine
Menhaden	*Brevortia tyrannus*	haul-seine
Pinfish	*Lagodon rhomboides*	haul-seine
Cownose ray	*Rhinoptera bonasus*	haul-seine
Black drum	*Pogonias cromis*	both
Spotted trout	*Cynoscion nebulosus*	both
Striped mullet	*Mugil cephalus*	prey seine
Red drum	*Sciaenops ocellatus*	both
Oyster toadfish	*Opsanus tau*	both
Spanish mackeral	*Scomberomorus maculatus*	haul-seine
Atlantic thread herring	*Opisthonema oglinum*	both
Butterfish	*Peprilus triacanthus*	haul-seine
Pigfish	*Orthopristis chrysoptera*	haul-seine
Northern kingfish	*Menticirrhus saxatilis*	haul-seine
Sandbar shark	*Carcharinus plumbeus*	haul-seine
Houndfish	*Tylosurus crocodilus*	haul-seine
Northern puffer	*Sphoeriodes maculatus*	both
Spadefish	*Chaetodipterus faber*	both
Striped burrfish	*Chilomycterus schoepfi*	haul-seine
White perch	*Morone americana*	haul-seine
Tautog	*Tautoga onitus*	haul-seine

Table 2.2. The total number and biomass of all species captured in the prey seine May-November 2001 are given in order of decreasing abundance. Data represents twelve prey seine samples taken in conjunction with haul-seine sampling. Gear efficiency measures have not been applied therefore this data should not be considered a depiction of relative abundance. The Reg. column below is total length wet weight regression where y is wet weight (gm) and x is total length (mm). Blue crab regression is based on carapace width.

SPECIES	NO. CAUGHT	TOTAL BIOMASS(GM)	REG. (Y=GM WET), X=MM)	R^2	SIZE (MM)	N
Blue crab	1668	11313	$y=1E-04x^{2.8346}$	0.9941	11-41	28
Atlantic silverside	650	1077.1	$y=1E-05x^{2.8069}$	0.9639	42-104	91
Silver perch	536	891.5	$y=9E-06x^{3.0906}$	0.9885	26-110	45
Bay anchovy	484	496.5	$y=2E-05x^{2.6988}$	0.8005	57-67	16
Mummichog	379	1527.1	$y=1E-06x^{3.6041}$	0.99	44-89	19
Striped killifish	220	1155.8	$y=6E-06x^{3.1701}$	0.9711	31-115	119
Rainwater killifish	178	94	$y=4E-06x^{3.2943}$	0.977	19-50	91
Naked goby	128	95.9	$y=5E-06x^{3.2076}$	0.9819	17-54	95
Spot	90	4135.9	$y=6E-06x^{3.1649}$	0.9967	74-274	51
Northern pipefish	38	56.1	$y=7E-08x^{3.3439}$	0.9972	78-184	8
Oyster toadfish	25	256.9	$y=9E-06x^{3.1042}$	0.9981	48-153	13
Skilletfish	16	23.4	$y=2E-04x^{2.3832}$	0.9081	22-54	13
Red drum	15	1575.4	$y=6E-06x^{3.0643}$	0.9892	39-60	11
Fourspine stickleback	15	8.3	$y=2E-05x^{2.7337}$	0.8987	32-51	15
Striped blenny	10	31.7	$y=6E-06^{3.1997}$	0.978	52-81	9
Spotted trout	9	13.2				
Dusky pipefish	8	12.8	$y=3E-10x^{4.5592}$	0.8992	86-118	6
Southern flounder	7	217.5				
American eel	6	546.5				
Striped mullet	5	939.5				
Thread fin herring	5	546.4				
Striped bass	4	2.1				
Feather blenny	3	11				
Halfbeak	3	39.1				
Atlantic needlefish	3	50				
Black drum	2	173.2				
Northern puffer	2	196				
Spadefish	2	2.7				
Winter flounder	2	3.5				
Chain pipefish	2	173.2				
Hogchoker	1	37				
Striped anchovy	1	3.7				
Sheepshead	1	1				
33 species total						

Table 2.3. Date of sample, species abundance, biomass, average fish's mass, and the gear efficiency used to estimate the number and biomass per square meter are given below. All samples were taken at mid-tide during the day. Species are arranged in order of descending abundance. Abundance and biomass densities per haul are summed below each sample period.

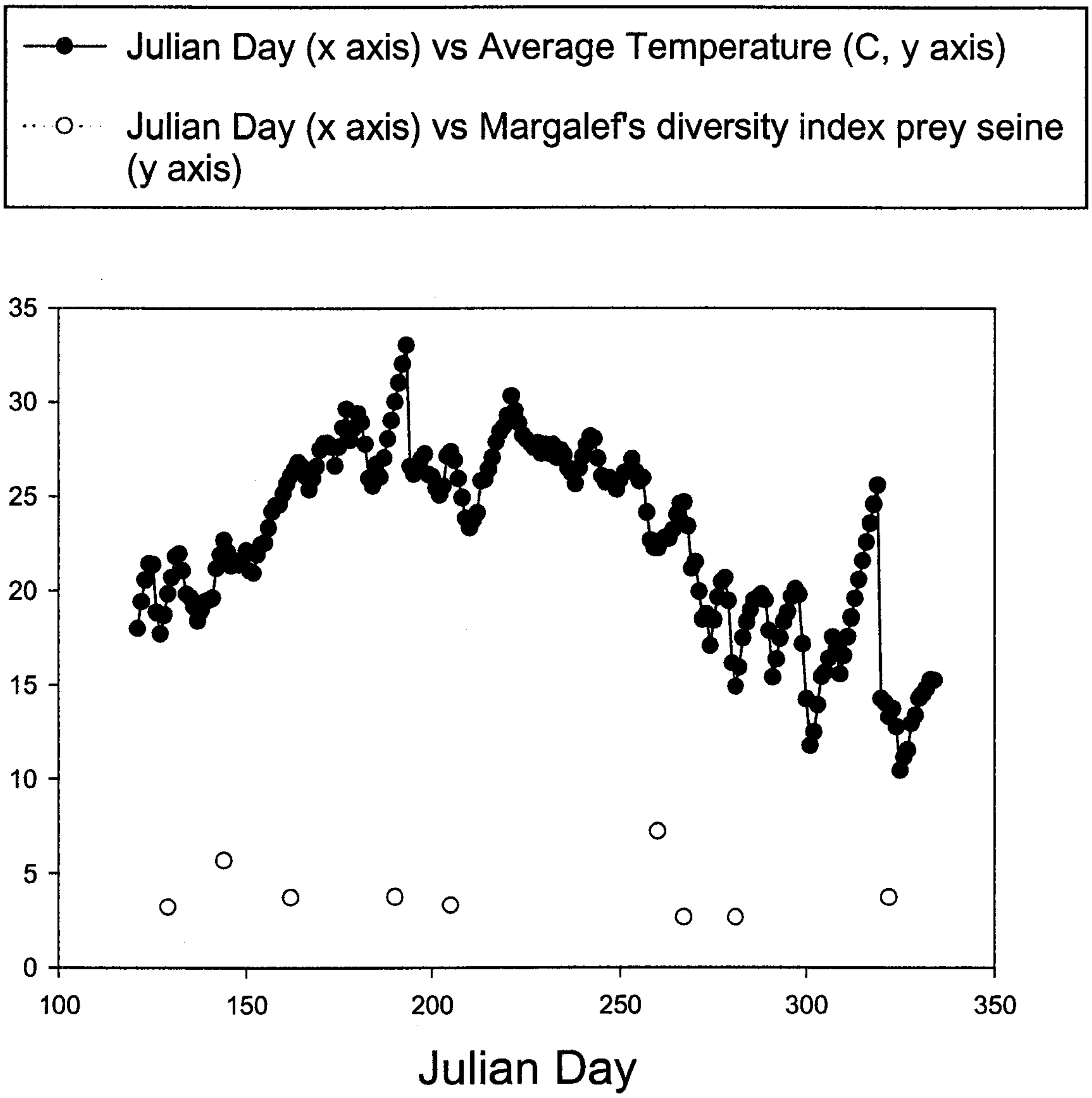
Date	Species	No.	Biomass (gm)	Average Mass/ Fish	Gear Efficiency	Number/ m^2	Grams/ m^2
4/25/01	Striped killifish	34	95.1	2.8	69	1.40E-01	3.92E-01
4/25/01	Blue crab	28	23.2	0.8	38	2.09E-01	1.73E-01
4/25/01	Naked goby	3	3.3	1.1	57	1.50E-02	1.62E-02
4/25/01	Mummichog	2	1.9	1.0	54	1.05E-02	1.00E-02
4/25/01	Northern pipefish	1	3.0	3.0	57	4.98E-03	1.50E-02
4/25/01	Rainwater killifish	1	0.5	0.5	57	4.98E-03	2.54E-03
					Density sums	3.85E-01	6.09E-01
5/10/01	Bay anchovy	433	428.0	1.0	57	2.16E+00	2.13E+00
5/10/01	Blue crab	84	397.0	4.7	38	6.28E-01	2.97E+00
5/10/01	Mummichog	78	134.8	1.7	54	4.10E-01	7.09E-01
5/10/01	Northern pipefish	10	21.6	2.2	57	4.98E-02	1.08E-01
5/10/01	Rainwater killifish	5	4.7	0.9	57	2.49E-02	2.36E-02
5/10/01	Atlantic silverside	4	12.0	3.0	69	1.65E-02	4.93E-02
5/10/01	Naked goby	3	3.4	1.1	57	1.50E-02	1.68E-02
5/10/01	Striped killifish	3	3.2	1.1	69	1.24E-02	1.30E-02
5/10/01	Sheepshead	1	1.0	1.0	57	4.98E-03	4.98E-03
5/10/01	American eel	1	0.4	0.4	57	4.98E-03	1.94E-03
					Density sums	3.32E+00	6.03E+00
5/25/01	Blue crab	346	3059.0	8.8	38	2.59E+00	2.29E+01
5/25/01	Naked goby	33	42.6	1.3	57	1.64E-01	2.12E-01
5/25/01	Bay anchovy	15	17.6	1.2	57	7.48E-02	8.79E-02
5/25/01	Spot	9	20.7	2.3	57	4.49E-02	1.03E-01
5/25/01	Mummichog	7	30.9	4.4	54	3.68E-02	1.63E-01
5/25/01	Striped killifish	6	35.7	6.0	69	2.47E-02	1.47E-01
5/25/01	Summer flounder	5	9.2	1.8	57	2.49E-02	4.60E-02
5/25/01	Atlantic silverside	4	15.2	3.8	69	1.65E-02	6.24E-02
5/25/01	Northern pipefish	3	5.8	1.9	57	1.50E-02	2.88E-02
5/25/01	Winter flounder	2	3.5	1.8	57	9.97E-03	1.73E-02
5/25/01	Striped bass	2	1.0	0.5	57	9.97E-03	4.98E-03
5/25/01	American eel	1	310.0	310.0	57	4.98E-03	1.55E+00
5/25/01	Hogchoker	1	37.0	37.0	57	4.98E-03	1.84E-01
5/25/01	Feather blenny	1	7.3	7.3	57	4.98E-03	3.64E-02
5/25/01	Striped blenny	1	3.1	3.1	57	4.98E-03	1.55E-02
5/25/01	Skilletfish	1	1.0	1.0	57	4.98E-03	5.08E-03
					Density sums	3.03E+00	2.55E+01
6/12/01	Blue crab	363	1221.7	3.4	38	2.71E+00	9.13E+00
6/12/01	Mummichog	57	177.0	3.1	54	3.00E-01	9.31E-01
6/12/01	Spot	21	45.4	2.2	57	1.05E-01	2.26E-01

6/12/01	Northern pipefish	14	15.3	1.1	57	6.98E-02	7.62E-02
6/12/01	Atlantic silverside	12	11.3	0.9	69	4.94E-02	4.65E-02
6/12/01	Striped killifish	6	41.4	6.9	69	2.47E-02	1.70E-01
6/12/01	Rainwater killifish	5	5.1	1.0	57	2.49E-02	2.54E-02
6/12/01	Oyster toadfish	3	40.5	13.5	57	1.50E-02	2.02E-01
6/12/01	Naked goby	2	2.8	1.4	57	9.97E-03	1.41E-02
6/12/01	Striped bass	2	1.1	0.6	57	9.97E-03	5.58E-03
6/12/01	Dusky pipefish	1	2.9	2.9	57	4.98E-03	1.45E-02
					Density sums	3.33E+00	1.08E+01
7/10/01	Mummichog	158	776.0	4.9	54	8.31E-01	4.08E+00
7/10/01	Blue crab	121	622.1	5.1	38	9.05E-01	4.65E+00
7/10/01	Silver perch	80	40.6	0.5	57	3.99E-01	2.02E-01
7/10/01	Atlantic silverside	53	35.2	0.7	69	2.18E-01	1.45E-01
7/10/01	Rainwater killifish	29	25.4	0.9	57	1.45E-01	1.27E-01
7/10/01	Striped killifish	8	48.6	6.1	69	3.29E-02	2.00E-01
7/10/01	Atlantic needlefish	3	50.0	16.7	57	1.50E-02	2.49E-01
7/10/01	Northern pipefish	3	4.3	1.4	57	1.50E-02	2.14E-02
7/10/01	Naked goby	2	3.0	1.5	57	9.97E-03	1.50E-02
7/10/01	Dusky pipefish	1	7.2	7.2	57	4.98E-03	3.57E-02
7/10/01	Spot	1	2.6	2.6	57	4.98E-03	1.27E-02
					Density sums	2.58E+00	9.74E+00
7/25/01	Silver perch	410	615.2	1.5	57	2.04E+00	3.07E+00
7/25/01	Blue crab	234	2692.0	11.5	38	1.75E+00	2.01E+01
7/25/01	Atlantic silverside	209	384.5	1.8	69	8.61E-01	1.58E+00
7/25/01	Striped killifish	68	434.4	6.4	69	2.80E-01	1.79E+00
7/25/01	Mummichog	58	258.3	4.5	54	3.05E-01	1.36E+00
7/25/01	Rainwater killifish	26	16.7	0.6	57	1.30E-01	8.32E-02
7/25/01	Spot	21	285.7	13.6	57	1.05E-01	1.42E+00
7/25/01	Oyster toadfish	2	0.6	0.3	57	9.97E-03	2.79E-03
7/25/01	American eel	1	148.0	148.0	57	4.98E-03	7.38E-01
7/25/01	Naked goby	1	1.0	1.0	57	4.98E-03	4.98E-03
7/25/01	Striped blenny	1	0.2	0.2	57	4.98E-03	8.97E-04
					Density sums	5.50E+00	3.02E+01
8/28/01	Atlantic silverside	169	204.2	1.2	69	6.96E-01	8.41E-01
8/28/01	Blue crab	166	501.9	3.0	38	1.24E+00	3.75E+00
8/28/01	Rainwater killifish	111	41.3	0.4	57	5.53E-01	2.06E-01
8/28/01	Naked goby	76	32.3	0.4	57	3.79E-01	1.61E-01
8/28/01	Striped killifish	57	287.1	5.0	69	2.35E-01	1.18E+00
8/28/01	Silver perch	30	79.9	2.7	57	1.50E-01	3.98E-01
8/28/01	Spot	26	3205.6	123.3	57	1.30E-01	1.60E+01
8/28/01	Fourspine stickleback	13	6.6	0.5	57	6.48E-02	3.30E-02
8/28/01	Skilletfish	10	14.7	1.5	57	4.98E-02	7.34E-02
8/28/01	Oyster toadfish	7	212.2	30.3	57	3.49E-02	1.06E+00
8/28/01	Northern pipefish	7	6.1	0.9	57	3.49E-02	3.03E-02
8/28/01	Striped blenny	6	16.7	2.8	57	2.99E-02	8.34E-02

8/28/01	Atlantic thread herring	5	546.9	109.4	57	2.49E-02	2.73E+00
8/28/01	Dusky pipefish	4	1.9	0.5	57	1.99E-02	9.47E-03
8/28/01	Striped mullet	3	809.6	269.9	57	1.50E-02	4.04E+00
8/28/01	American eel	3	88.1	29.4	57	1.50E-02	4.39E-01
8/28/01	Northern puffer	1	96.9	96.9	57	4.98E-03	4.83E-01
					Density sums	3.68E+00	3.15E+01
9/18/01	Blue crab	189	2426.0	12.8	38	1.41E+00	1.81E+01
9/18/01	Atlantic silverside	137	280.0	2.0	69	5.64E-01	1.15E+00
9/18/01	Bay anchovy	36	50.9	1.4	57	1.79E-01	2.54E-01
9/18/01	Striped killifish	18	67.3	3.7	69	7.41E-02	2.77E-01
9/18/01	Silver perch	15	145.6	9.7	57	7.48E-02	7.26E-01
9/18/01	Spot	12	540.2	45.0	57	5.98E-02	2.69E+00
9/18/01	Oyster toadfish	4	12.7	3.2	57	1.99E-02	6.32E-02
9/18/01	Halfbeak	3	39.1	13.0	57	1.50E-02	1.95E-01
9/18/01	Spotted trout	3	6.3	2.1	50	1.70E-02	3.55E-02
9/18/01	Red drum	2	1563.6	781.8	84	6.76E-03	5.29E+00
9/18/01	Summer flounder	2	208.3	104.1	57	9.97E-03	1.04E+00
9/18/01	Striped blenny	2	11.7	5.8	57	9.97E-03	5.81E-02
9/18/01	Naked goby	2	2.9	1.5	57	9.97E-03	1.45E-02
9/18/01	Spadefish	2	2.7	1.4	57	9.97E-03	1.35E-02
9/18/01	Northern puffer	1	99.1	99.1	57	4.98E-03	4.94E-01
9/18/01	Black drum	1	87.3	87.3	57	4.98E-03	4.35E-01
9/18/01	Chain pipefish	1	87.3	87.3	57	4.98E-03	4.35E-01
9/18/01	Striped anchovy	1	3.7	3.7	57	4.98E-03	1.84E-02
9/18/01	Feather blenny	1	1.8	1.8	57	4.98E-03	8.97E-03
9/18/01	Skilletfish	1	0.3	0.3	57	4.98E-03	1.57E-03
					Density sums	2.49E+00	3.13E+01
9/25/01	Blue crab	79	203.0	2.6	38	5.91E-01	1.52E+00
9/25/01	Atlantic silverside	23	40.8	1.8	69	9.47E-02	1.68E-01
9/25/01	Striped killifish	14	58.7	4.2	69	5.76E-02	2.42E-01
9/25/01	Mummichog	4	28.7	7.2	54	2.10E-02	1.51E-01
9/25/01	Skilletfish	3	6.2	2.1	57	1.50E-02	3.10E-02
9/25/01	Spot	2	35.7	17.9	57	9.97E-03	1.78E-01
9/25/01	Silver perch	1	10.2	10.2	57	4.98E-03	5.08E-02
9/25/01	Naked goby	1	0.6	0.6	57	4.98E-03	2.89E-03
					Density sums	7.99E-01	2.34E+00
10/09/01	Blue crab	39	93.8	2.4	38	2.92E-01	7.01E-01
10/09/01	Mummichog	13	50.6	3.9	54	6.84E-02	2.66E-01
10/09/01	Atlantic silverside	12	25.3	2.1	69	4.94E-02	1.04E-01
10/09/01	Spotted trout	6	7.0	1.2	50	3.41E-02	3.96E-02
10/09/01	Naked goby	5	4.1	0.8	57	2.49E-02	2.03E-02
10/09/01	Striped killifish	1	5.7	5.7	69	4.12E-03	2.36E-02
					Density sums	4.72E-01	1.15E+00

10/30/01	Atlantic silverside	20	50.4	2.5	69	8.23E-02	2.08E-01
10/30/01	Striped killifish	12	26.5	2.2	69	4.94E-02	1.09E-01
10/30/01	Blue crab	11	60.7	5.5	38	8.22E-02	4.54E-01
10/30/01	Mummichog	8	47.6	6.0	54	4.21E-02	2.50E-01
10/30/01	Striped mullet	2	129.9	64.9	57	9.97E-03	6.47E-01
10/30/01	Black drum	1	85.9	85.9	57	4.98E-03	4.28E-01
10/30/01	Chain pipefish	1	85.9	85.9	57	4.98E-03	4.28E-01
10/30/01	Feather blenny	1	1.9	1.9	57	4.98E-03	9.22E-03
10/30/01	Skilletfish	1	1.1	1.1	57	4.98E-03	5.43E-03
10/30/01	Fourspine stickleback	1	0.8	0.8	57	4.98E-03	3.89E-03
10/30/01	Red drum	1	0.5	0.5	84	3.38E-03	1.69E-03
10/30/01	Dusky pipefish	1	0.2	0.2	57	4.98E-03	7.97E-04
					Density sums	2.99E-01	2.55E+00
11/19/01	Striped killifish	16	52.3	3.3	69	6.59E-02	2.15E-01
11/19/01	Red drum	12	11.3	0.9	84	4.06E-02	3.83E-02
11/19/01	Blue crab	8	13.6	1.7	38	5.98E-02	1.02E-01
11/19/01	Atlantic silverside	7	18.3	2.6	69	2.88E-02	7.51E-02
11/19/01	Mummichog	1	21.3	21.3	54	5.26E-03	1.12E-01
11/19/01	Fourspine stickleback	1	0.9	0.9	57	4.98E-03	4.59E-03
11/19/01	Dusky pipefish	1	0.6	0.6	57	4.98E-03	3.19E-03
11/19/01	Rainwater killifish	1	0.2	0.2	57	4.98E-03	7.97E-04
					Density sums	2.15E-01	5.51E-01

Figure 2.5. This figure provides the Margalef's diversity index for prey seine samples and a graph of seasonal temperature at the study site.



4). Margalef's diversity index varied seasonally as species diversity and total abundance fluctuated. Small peaks in the index were evident in the spring and fall, presumably due to various species immigrating and emigrating through the site and a lower total abundance.

Crustaceans significantly contributed to prey seine biomass and abundance. Unfortunately, shrimp were so numerous and difficult to separate from macroalgae and floating grass that they were not collected. In retrospect, this practice was an oversight. Blue crab dominated total biomass and abundance across the sample period.

Resident mummichog and striped killifish dominated spring and fall finfish biomass. A spring influx of larger naked goby and a late summer early fall increase in the relative abundance of Atlantic siverside was evident. The sporadic nature of bay anchovy's appearance in samples was noteworthy but not surprising. A single large catch occurred in the spring. The importance of this sample should be viewed with some scrutiny, however, because the species visually schools during daylight hours, a fact that likely biased gear's performance. YOY silver perch and spot showed clear patterns of immigration, emigration, and residence. Juvenile silver perch appeared in large numbers in early July, dominated finfish biomass by late July, and stayed in the region until late September. Although a few spot were captured in late May (earlier than silver perch), they were not large and plentiful enough to be the biomass dominant until August. At this time, however, their biomass exceeded that of blue crabs. This is the only time during mid-season crab residence that the biomass of a finfish contributed more to total biomass. Spot continued to significantly contribute to biomass until late September when finfish dominance reverted back to resident Fundulus species.

Incidental capture of larger specimens in prey seine gear should be mentioned to avoid misinterpretation of biomass data. Biomass contributions of red drum, American eel, striped mullet, and Atlantic needlefish at first glance appear significant on several dates but contributions in most cases were due to capture of a few large fish. No gear efficiencies for larger fish of any species were determined for prey seine. Caution should be exercised in application of density data if due to large fish.

Prey seine littoral samples reveal a significant diversity of YOY species including many commercially and recreationally important fishes. Striped bass YOY were captured in May and June. Spotted trout and red drum YOY showed patterns of fall immigration, with trout preceding drum. Small YOY winter and summer flounder were both captured in early spring and larger YOY summer flounder were captured in both seines in the fall. Spot showed clear patterns of nursery use and littoral production. A clear nursery pattern was also evident in silver perch. High densities of these two fishes suggest that they may be important to transient piscivores.

Haul-seine

The haul-seine catch consisted of 31 finfish species including southern stingrays (*Dasyatis americana*), Atlantic stingrays (*Dasyatis sabina*). Terrapins (*Malaclemys terrapin*) and horseshoe crabs (*Limulus polyphemus*) were also collected in samples but were immediately released. Unfortunately, misidentification on several occasions prevented conclusive separation of previously mentioned elasmobranches spp. Fourteen fish occurred in large enough numbers to derive meaningful length x weight regressions (Table 2.4). Catches were highly variable in assemblage structure (Table 2.5) due to temporal fluctuations in individual species biomass and abundance. Graphs of seasonal abundance and biomass for the ten most abundant species captured in the haul-seine can be found in Appendix 5. Size distributions for the six most abundant species can be found in Appendix 6.

Gizzard shad dominated abundance and biomass across catches and peaked in mid-summer. Croaker was the second most abundant species. Croaker biomass dominated for a short time in early spring and reached peak abundance and biomass in mid-summer (July). Some species like striped bass and hickory shad showed expected seasonal abundance peaks in spring and fall. Gizzard shad demonstrated a much higher abundance and biomass than expected throughout the study period. Species' assemblage structure was most diverse in September (18) and lowest in the early spring (6). Early fall species diversity in haul-seine, like that found in the late

Table 2.4. The total number and biomass of all species captured in the haul-seine April-November 2001 are given in order of decreasing abundance. Data represents fourteen seine samples taken during both day and night hauls. Gear efficiency data has not been applied therefore table should not be considered a depiction of relative abundance. The Reg. column below is total length wet weight regression where y is wet weight (gm) and x is total length (mm).

SPECIES	NUMBER CAUGHT	TOTAL BIOMASS (GM)	REG. (Y=GM WET, X=MM)	R^2	SIZE (MM)	N
Gizzard shad	30503	18308108	$y=5E\text{-}07x^{3.5277}$	0.9252	344-428	38
Croaker	15825	6693478	$y=2E\text{-}05x^{2.9209}$	0.9476	200-432	239
Spot	2735	424240	$y=5E\text{-}06x^{3.2155}$	0.9921	74-324	264
Striped bass	1033	592976	$y=1E\text{-}05x^{2.9636}$	0.974	231-1017	297
Bluefish	312	137297	$y=4E\text{-}05x^{2.7477}$	0.9597	156-498	221
Weakfish	303	104711	$y=5E\text{-}05x^{2.7252}$	0.9499	247-645	190
Silver perch	164	20343	$y=6E\text{-}06x^{3.1758}$	0.9976	26-235	142
Summer flounder	60	23508	$y=8E\text{-}06x^{3.0601}$	0.9933	171-450	34
Hickory shad	37	17590.9	$y=3E\text{-}05x^{2.7678}$	0.9542	296-388	18
Unknown rays	34	31130.8	$y=.01x^{3.16}$			
Menhaden	32	2862				
Pinfish	26	3089.3	$y=8E\text{-}05x^{2.7156}$	0.9683	158-236	20
Cownose ray	21	289108.5				
Black drum	17	3548	$y=1E\text{-}05x^{3.0103}$	0.9695	174-247	12
Spotted trout	16	6056	$y=8E\text{-}06x^{3.0439}$	0.9989	50-580	26
Striped mullet	12	1610.8				
Red drum	11	8477	$y=4E\text{-}06x^{3.1987}$	0.9997	39-640	23
Oyster toadfish	9	986.4				
Spanish mackeral	8	6675.3				
Thread fin herring	5	577.6				
Butterfish	5	304.4				
Pigfish	5	682				
Northern kingfish	3	929.8				
Sandbar shark	3	6277.6				
Houndfish	3	2400				
Northern puffer	2	449.3				
Spadefish	2	6.3				
Striped burrfish	2	159.4				
White perch	2	151				
Tautog	1	120				
32 species						

Table 2.5. Table 2.5 gives the population and biomass data per square meter for each species captured in the haul-seine. Species are arranged in order of descending abundance. The date of each daytime sample is followed by the letter D. Density estimates have been calculated using gear efficiencies given previously in chart 2.2. Abundance and biomass densities have been summed at the bottom of each sample.

Date	Species	No.	Biomass (gm)	Average Mass/ Fish	Gear Efficiency	Number/ m ^{2}	Grams/ m ^{2}
4/12/01D	Striped bass	11	19001.0	1727.4	54	1.41E-04	2.44E-01
					Density sums	1.41E-04	2.44E-01
4/25/01D	Croaker	91	53235.0	585.0	50	1.26E-03	7.37E-01
4/25/01D	Gizzard shad	13	8274.0	636.5	41	2.19E-04	1.40E-01
4/25/01D	Hickory shad	17	9133.0	537.2	54	2.18E-04	1.17E-01
4/25/01D	Striped bass	1	2850.0	2850.0	54	1.28E-05	3.65E-02
4/25/01D	Summer flounder	1	690.0	690.0	20	3.46E-05	2.39E-02
4/25/01D	Spot	1	296.9	296.9	62	1.12E-05	3.31E-03
					Density sums	1.76E-03	1.06E+00
5/10/01	Croaker	3764	1568082.4	416.6	50	5.21E-02	2.17E+01
5/10/01	Gizzard shad	2317	1473612.0	636.0	41	3.91E-02	2.49E+01
5/10/01	Spot	422	76431.2	181.1	62	4.71E-03	8.53E-01
5/10/01	Striped bass	91	131999.0	1450.5	54	1.17E-03	1.69E+00
5/10/01	Bluefish	87	50385.6	579.1	54	1.12E-03	6.46E-01
5/10/01	Weakfish	36	18575.0	516.0	54	4.61E-04	2.38E-01
5/10/01	Silver perch	8	828.1	103.5	54	1.03E-04	1.06E-02
5/10/01	Oyster toadfish	7	791.9	113.1	20	2.42E-04	2.74E-02
5/10/01	Rays	3	8841.6	2947.2	54	3.85E-05	1.13E-01
5/10/01	Summer flounder	3	1650.0	550.0	20	1.04E-04	5.71E-02
5/10/01	Black drum	1	1179.0	1179.0	50	1.38E-05	1.63E-02
5/10/01	Tautog	1	120.0	120.0	54	1.28E-05	1.54E-03
5/10/01	Hickory shad	1	116.2	116.2	54	1.28E-05	1.49E-03
					Density sums	9.92E-02	5.02E+01
5/25/01	Croaker	2440	1016659.1	416.7	50	3.38E-02	1.41E+01
5/25/01	Gizzard shad	1824	890516.8	488.2	41	3.08E-02	1.50E+01
5/25/01	Spot	386	55379.5	143.5	62	4.31E-03	6.18E-01
5/25/01	Bluefish	23	18981.0	825.3	54	2.95E-04	2.43E-01
5/25/01	Silver perch	17	2163.8	127.3	54	2.18E-04	2.77E-02
5/25/01	Cownose ray	16	239379.8	14961.2	90	1.23E-04	1.84E+00
5/25/01	Striped bass	16	17197.0	1074.8	54	2.05E-04	2.20E-01
5/25/01	Summer flounder	11	7065.9	642.4	20	3.81E-04	2.45E-01
5/25/01	Rays	11	5270.9	479.2	54	1.41E-04	6.76E-02
5/25/01	Weakfish	10	2887.0	288.7	54	1.28E-04	3.70E-02
5/25/01	Hickory shad	5	1921.6	384.3	54	6.41E-05	2.46E-02
5/25/01	Spanish mackeral	3	2188.7	729.6	54	3.85E-05	2.81E-02
5/25/01	Menhaden	3	193.5	64.5	20	1.04E-04	6.70E-03
5/25/01	Houndfish	2	2400.0	1200.0	54	2.56E-05	3.08E-02
5/25/01	Red drum	1	1353.5	1353.5	57	1.21E-05	1.64E-02
5/25/01	Pinfish	1	152.0	152.0	71	9.75E-06	1.48E-03
					Density sums	7.06E-02	3.25E+01

6/12/01	Gizzard shad	3786	1848408.2	488.2	41	6.39E-02	3.12E+01
6/12/01	Croaker	3730	1688081.4	452.6	50	5.16E-02	2.34E+01
6/12/01	Spot	279	45395.3	162.7	62	3.11E-03	5.07E-01
6/12/01	Bluefish	51	17062.1	334.6	54	6.54E-04	2.19E-01
6/12/01	Striped bass	45	51239.0	1138.6	54	5.77E-04	6.57E-01
6/12/01	Silver perch	9	1021.5	113.5	54	1.15E-04	1.31E-02
6/12/01	Rays	8	11253.9	1406.7	54	1.03E-04	1.44E-01
6/12/01	Weakfish	8	2086.0	260.8	54	1.03E-04	2.67E-02
6/12/01	Menhaden	3	193.5	64.5	20	1.04E-04	6.70E-03
6/12/01	Summer flounder	2	912.5	456.3	20	6.92E-05	3.16E-02
6/12/01	Striped mullet	1	228.5	228.5	20	3.46E-05	7.91E-03
6/12/01	Spanish mackeral	1	302.8	302.8	54	1.28E-05	3.88E-03
6/12/01	Thread herring	1	86.8	86.8	20	3.46E-05	3.00E-03
6/12/01	Pinfish	1	78.7	78.7	71	9.75E-06	7.67E-04
					Density sums	1.20E-01	5.62E+01
6/19/01D	Gizzard shad	179	112233.0	627.0	41	3.02E-03	1.89E+00
6/19/01D	Croaker	41	18840.9	459.5	50	5.68E-04	2.61E-01
6/19/01D	Silver perch	11	1610.8	146.4	54	1.41E-04	2.06E-02
6/19/01D	Bluefish	4	1061.4	265.4	54	5.13E-05	1.36E-02
6/19/01D	Spanish mackeral	2	972.9	486.5	54	2.56E-05	1.25E-02
6/19/01D	Weakfish	1	1613.0	1613.0	54	1.28E-05	2.07E-02
6/19/01D	Sandbar shark	1	511.6	511.6	54	1.28E-05	6.56E-03
6/19/01D	Striped bass	0	0.0	0.0	54	0.00E+00	0.00E+00
					Density sums	3.83E-03	2.23E+00
7/10/01	Gizzard shad	7659	4802193.0	627.0	41	1.29E-01	8.11E+01
7/10/01	Croaker	3546	1449333.6	408.7	50	4.91E-02	2.01E+01
7/10/01	Spot	611	114585.4	187.5	62	6.82E-03	1.28E+00
7/10/01	Weakfish	39	13977.0	358.4	54	5.00E-04	1.79E-01
7/10/01	Bluefish	28	9161.5	327.2	54	3.59E-04	1.17E-01
7/10/01	Striped bass	25	8384.0	335.4	54	3.20E-04	1.07E-01
7/10/01	Summer flounder	11	2749.0	249.9	20	3.81E-04	9.51E-02
7/10/01	Silver perch	9	877.1	97.5	54	1.15E-04	1.12E-02
7/10/01	Menhaden	5	322.5	64.5	20	1.73E-04	1.12E-02
7/10/01	Pinfish	3	423.6	141.2	71	2.92E-05	4.13E-03
7/10/01	Striped mullet	1	306.0	306.0	20	3.46E-05	1.06E-02
7/10/01	Spotted trout	1	538.7	538.7	54	1.28E-05	6.91E-03
					Density sums	1.87E-01	1.03E+02
7/25/01	Gizzard shad	5497	3446619.0	627.0	41	9.28E-02	5.82E+01
7/25/01	Croaker	1725	700860.6	406.3	50	2.39E-02	9.70E+00
7/25/01	Spot	629	76769.2	122.0	62	7.02E-03	8.57E-01
7/25/01	Bluefish	50	17489.0	349.8	54	6.41E-04	2.24E-01
7/25/01	Striped bass	37	26543.0	717.4	54	4.74E-04	3.40E-01
7/25/01	Weakfish	37	11239.0	303.8	54	4.74E-04	1.44E-01
7/25/01	Silver perch	35	3569.4	102.0	54	4.49E-04	4.58E-02
7/25/01	Summer flounder	9	1091.8	121.3	20	3.11E-04	3.78E-02
7/25/01	Rays	8	3547.4	443.4	54	1.03E-04	4.55E-02
7/25/01	Menhaden	5	322.5	64.5	20	1.73E-04	1.12E-02

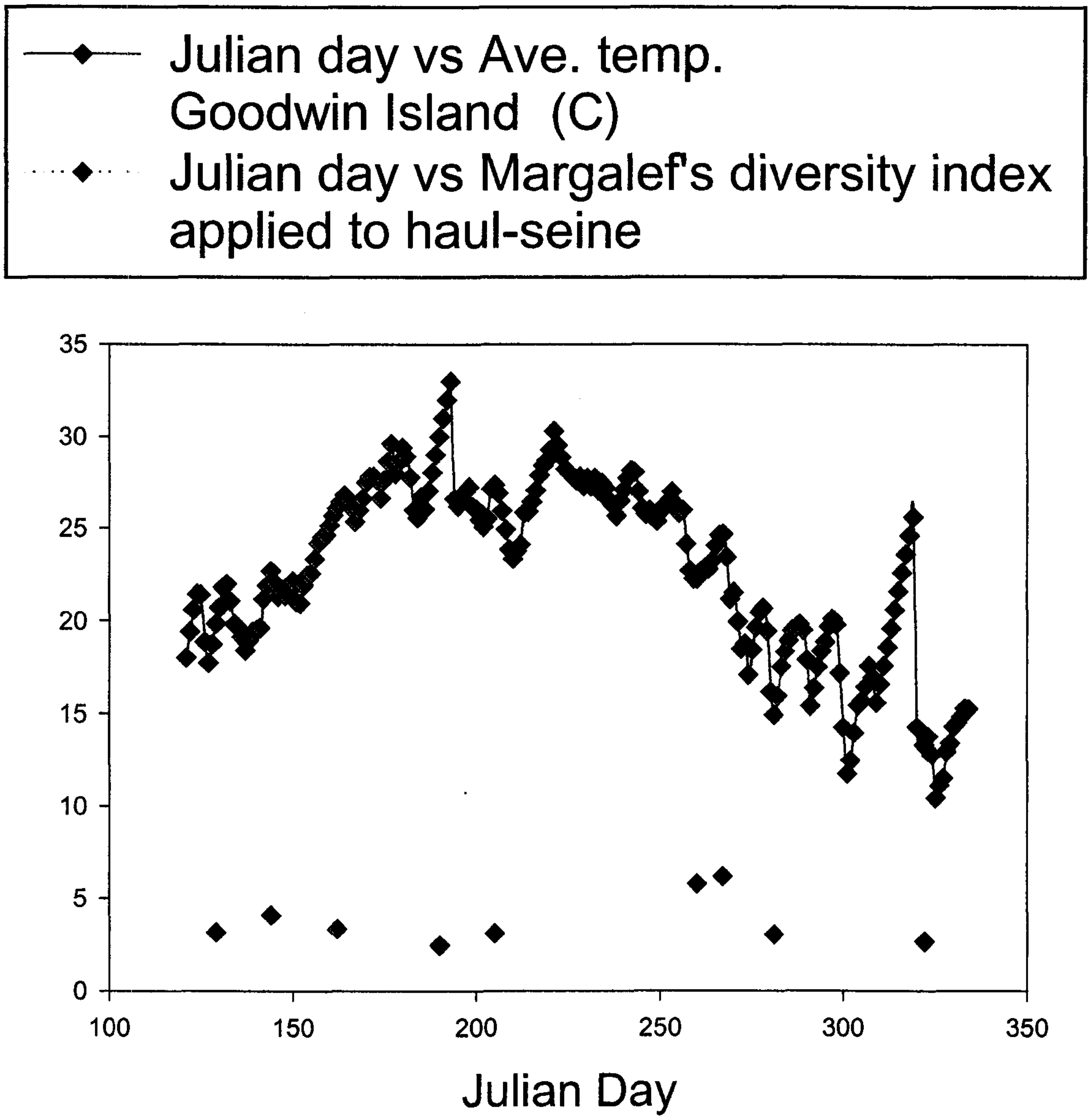
7/25/01	Cownose ray	5	0.0	0.0	90	3.85E-05	0.00E+00
7/25/01	Oyster toadfish	2	194.5	97.3	20	6.92E-05	6.73E-03
7/25/01	Sandbar shark	1	2861.0	2861.0	54	1.28E-05	3.67E-02
					Density sums	1.26E-01	6.96E+01
8/28/01D	Gizzard shad	1272	797544.0	627.0	41	2.15E-02	1.35E+01
8/28/01D	Croaker	481	195428.4	406.3	50	6.66E-03	2.71E+00
8/28/01D	Weakfish	9	2982.0	331.3	54	1.15E-04	3.82E-02
8/28/01D	Silver perch	8	856.2	107.0	54	1.03E-04	1.10E-02
8/28/01D	Striped mullet	7	237.7	34.0	20	2.42E-04	8.23E-03
8/28/01D	Striped bass	5	6848.0	1369.6	54	6.41E-05	8.78E-02
8/28/01D	Summer flounder	5	2526.5	505.3	20	1.73E-04	8.74E-02
8/28/01D	Rays	5	2217.0	443.4	54	6.41E-05	2.84E-02
8/28/01D	Pigfish	4	349.0	87.3	54	5.13E-05	4.47E-03
8/28/01D	Bluefish	2	777.9	389.0	54	2.56E-05	9.97E-03
8/28/01D	Striped burrfish	2	159.4	79.7	20	6.92E-05	5.52E-03
8/28/01D	Spot	2	288.0	144.0	62	2.23E-05	3.22E-03
8/28/01D	Spadefish	2	6.3	3.2	20	6.92E-05	2.18E-04
8/28/01D	Northern puffer	1	134.0	134.0	20	3.46E-05	4.64E-03
8/28/01D	Spotted trout	1	169.0	169.0	54	1.28E-05	2.17E-03
					Density sums	2.92E-02	1.65E+01
9/18/01	Gizzard shad	500	313500.0	627.0	41	8.44E-03	5.29E+00
9/18/01	Spot	174	17049.9	98.0	62	1.94E-03	1.90E-01
9/18/01	Weakfish	72	22453.0	311.8	54	9.23E-04	2.88E-01
9/18/01	Silver perch	53	7716.6	145.6	54	6.79E-04	9.89E-02
9/18/01	Bluefish	24	8206.5	341.9	54	3.08E-04	1.05E-01
9/18/01	Menhaden	16	1830.0	114.4	20	5.54E-04	6.33E-02
9/18/01	Summer flounder	5	1603.3	320.7	20	1.73E-04	5.55E-02
9/18/01	Spanish mackeral	4	3210.9	802.7	54	5.13E-05	4.12E-02
9/18/01	Croaker	4	1708.7	427.2	50	5.54E-05	2.37E-02
9/18/01	Thread herring	4	490.8	122.7	20	1.38E-04	1.70E-02
9/18/01	Red drum	2	1564.0	782.0	57	2.43E-05	1.90E-02
9/18/01	Northern puffer	2	219.9	110.0	20	6.92E-05	7.61E-03
9/18/01	Striped mullet	1	160.8	160.8	20	3.46E-05	5.57E-03
9/18/01	Pigfish	1	333.0	333.0	54	1.28E-05	4.27E-03
9/18/01	Spotted trout	1	269.3	269.3	54	1.28E-05	3.45E-03
9/18/01	Northern kingfish	1	265.0	265.0	54	1.28E-05	3.40E-03
9/18/01	Pinfish	1	220.0	220.0	71	9.75E-06	2.14E-03
9/18/01	Black drum	1	135.0	135.0	50	1.38E-05	1.87E-03
9/18/01	Striped bass	0	0.0	0.0	54	0.00E+00	0.00E+00
					Density sums	1.35E-02	6.22E+00
9/25/01	Gizzard shad	244	152988.0	627.0	41	4.12E-03	2.58E+00
9/25/01	Spot	160	20121.2	125.8	62	1.79E-03	2.25E-01
9/25/01	Weakfish	64	20315.0	317.4	54	8.20E-04	2.60E-01
9/25/01	Bluefish	35	10974.2	313.5	54	4.49E-04	1.41E-01
9/25/01	Pinfish	19	2215.0	116.6	71	1.85E-04	2.16E-02
9/25/01	Summer flounder	8	3542.8	442.9	20	2.77E-04	1.23E-01
9/25/01	Silver perch	8	1088.5	136.1	54	1.03E-04	1.40E-02

9/25/01	Cownose ray	5	49728.7	9945.7	90	3.85E-05	3.82E-01
9/25/01	Spotted trout	5	2747.0	549.4	54	6.41E-05	3.52E-02
9/25/01	Butterfish	5	304.4	60.9	20	1.73E-04	1.05E-02
9/25/01	Black drum	4	503.0	125.8	50	5.54E-05	6.96E-03
9/25/01	Croaker	3	1248.3	416.1	50	4.15E-05	1.73E-02
9/25/01	Striped mullet	2	418.4	209.2	20	6.92E-05	1.45E-02
9/25/01	Northern kingfish	2	664.8	332.4	54	2.56E-05	8.52E-03
9/25/01	Sandbar shark	1	2905.0	2905.0	54	1.28E-05	3.72E-02
9/25/01	Striped bass	1	1233.0	1233.0	54	1.28E-05	1.58E-02
9/25/01	Red drum	1	657.0	657.0	57	1.21E-05	7.98E-03
9/25/01	Northern puffer	1	95.4	95.4	20	3.46E-05	3.30E-03
					Density sums	4.16E-03	1.32E+00
10/09/01	Gizzard shad	3564	2234628.0	627.0	41	6.02E-02	3.77E+01
10/09/01	Striped bass	750	827962.0	1103.9	54	9.61E-03	1.06E+01
10/09/01	Spot	71	17923.3	252.4	62	7.93E-04	2.00E-01
10/09/01	Weakfish	8	2961.0	370.1	54	1.03E-04	3.80E-02
10/09/01	Summer flounder	5	1675.9	335.2	20	1.73E-04	5.80E-02
10/09/01	Bluefish	5	1612.2	322.4	54	6.41E-05	2.07E-02
10/09/01	Black drum	5	658.0	131.6	50	6.92E-05	9.11E-03
10/09/01	Silver perch	5	601.3	120.3	54	6.41E-05	7.71E-03
10/09/01	Red drum	3	2050.0	683.3	57	3.64E-05	2.49E-02
10/09/01	Striped mullet	2	259.4	129.7	20	6.92E-05	8.98E-03
10/09/01	Spotted trout	2	511.0	255.5	54	2.56E-05	6.55E-03
10/09/01	White perch	2	151.0	75.5	54	2.56E-05	1.94E-03
						7.12E-02	4.87E+01
10/30/01D	Gizzard shad	2725	1708575.0	627.0	41	4.60E-02	2.88E+01
10/30/01D	Striped bass	9	31396.0	3488.4	54	1.15E-04	4.02E-01
					Density sums	4.61E-02	2.92E+01
11/19/01	Gizzard shad	923	579018.0	627.3	41	1.56E-02	9.78E+00
11/19/01	Striped bass	43	63241.0	1470.7	54	5.51E-04	8.11E-01
11/19/01	Hickory shad	19	6420.2	337.9	54	2.44E-04	8.23E-02
11/19/01	Weakfish	19	5623.0	295.9	54	2.44E-04	7.21E-02
11/19/01	Spotted trout	6	1990.0	331.7	54	7.69E-05	2.55E-02
11/19/01	Black drum	6	973.0	162.2	50	8.31E-05	1.35E-02
11/19/01	Red drum	4	2853.0	713.3	57	4.86E-05	3.46E-02
11/19/01	Bluefish	3	1585.8	528.6	54	3.85E-05	2.03E-02
11/19/01	Silver perch	1	9.6	9.6	54	1.28E-05	1.23E-04
					Density sums	1.69E-02	1.08E+01

summer and early fall prey seine samples, was due to the collection of warm water and YOY fishes (striped mullet, pinfish, pigfish, spadefish, northern puffer, black drum, red drum, spotted trout, summer flounder). A significant interaction between Margalefs'diversity index and water temperature was not found (Fig. 2.6, Appendix 4). Margalef's diversity index for haul-seine catches was consistently less than that for the prey seine except for once in September. This high point in the haul-seine index followed peak prey diversity and coincided with a drastic decline in prey diversity.

A number of top-level predators were abundant in the study site seasonally. Houndfish, sandbar shark, Spanish mackerel, red drum, spotted trout, black drum, and summer flounder, (presented in order of increasing abundance) were collected. Large houndfish were only captured in the spring. Due to the extremely fusiform morphology of this species, it is likely not retained at small sizes. A large number of small individuals, presumably YOY and/or other *Belonidae* species, were observed in the site nocturnally in mid-summer but these fish were not susceptible to the gear. A single YOY sandbar shark so small that it still showed signs of yoke sac attachment was gilled in the haul-seine. This chance method of capture suggests that the gear's three-inch mesh may have been inadequate to quantify use YOY sandbar sharks. Larger shark specimens were collected in mid-summer and fall. Interestingly, Spanish mackerel, a fish generally recognized as a warm water pelagic predator, was captured in late spring and early summer. The rapid warming of the shallows may have provided a preferred habitat only at this time. In 2001, red drum were captured

Figure 2.6: The Margalef's diversity index of haul-seine catches and littoral temperature during sample is given below. Only haul-seine samples with corresponding prey seine samples were given below.



in the spring and fall. Haul seine catches in the study area in 2000 indicate, however, that occasional mid-summer usage does occur. Spotted trout occurred at low numbers sporadically throughout the summer. Peak abundance was in the fall but biomass was consistently low. A single juvenile black drum was captured in early spring and a much large number of YOY black drum were taken in the fall. Flounder of various sizes appeared throughout the study period. Larger fish were caught in the spring and YOY recruited to the haul-seine gear by mid-summer. YOY were gilled until late October.

Striped bass, Bluefish, and Weakfish

Diel differences

Diel comparisons between catches illustrated that all three piscivores occurred at a significantly greater abundance nocturnally. One hundred and eighty-nine striped bass were sampled during matched day/night comparison trials and 94.7 % of these were captured at night. The percentages of bluefish (n=171) and weakfish (n=145) caught at night were similar: 96.5% and 93.1% respectively. Chi-square analysis revealed that the probability of this outcome occurring was < .0001 for all three species.

Abundance and size and age distributions

Based on haul-seine samples striped bass, bluefish, and weakfish were by far the most abundant piscivores in the study area (Table 2.4). Striped bass dominated abundance and biomass of piscivores sampled. Striped bass biomass and abundance was greatest in early spring and fall when larger (older) migratory fishes joined the smaller presumably resident fish (Appendix 6, for size distribution; Appendix 7 for age). Patterns of size distribution and abundance mimic documented patterns of migration by older fish (emigration in spring and immigration in fall) and a support the hypothesis that these larger older fish prefer cooler water temperatures. As waters warmed, a trend of declining striped bass abundance occurred and average size and age declined. Surprisingly, some small fishes (200-325gm) continued to use the shallows into the summer, far beyond water temperatures that provided best growth potential (Hartman and Brandt, 1995b). Age 1 fish dominated catches during warmer months. By September, even small striped bass left the shallows. When the bass returned in October the largest sample size collected occurred, and its age composition resembled that sampled in early spring (May 10,2001). This apex in abundance occurred in October in both 2000 and 2001 suggesting that declining littoral water temperatures may act as an immigration cue. Interestingly, except for a few much older larger fish the last sample in November 19, 2001 also contained a large number of age 1 fish.

Bluefish were second to striped bass in abundance and biomass and their abundance and biomass was only slightly greater than that of weakfish. On average the bluefish captured in the study site were the youngest piscivores. No bluefish older than two were sampled and age 1 were by far the dominant. Bluefish abundance and biomass peaked in early spring. This catch contained by far the greatest number of larger (age 2) fish. Bluefish catches did not show a marked decline in abundance with increasing water temperatures. However, a shift towards smaller younger fish did occur in mid-summer. Early fall (Oct 10, 2001) samples evidenced drastic reductions in bluefish abundance. Average fish size increased in November but sample size was reduced further.

The breadth of weakfish ages sampled was second to that of striped bass. Early spring (May) and fall (Sept.) contained the oldest fish sampled and the largest diversity of age classes. Mid-summer samples consisted primarily of age 2 fish. A trend of increasing weakfish abundance and biomass occurred throughout the summer with largest samples (biomass and number) occurring in September. Age 2 dominated September samples. Weakfish numbers showed an even more marked decline than bluefish in October.

Predator and prey diversity correlations

Regression analysis demonstrated that no significant relationship existed between water temperature and the Margalef's diversity index of either gear (Appendix 4). Surprisingly, comparisons between gear diversity indices also indicated that no significant relationship existed between prey seine and haul-seine diversity (Appendix 8).

Predator-prey density correlations

Nocturnal predator densities and predator densities for all sampled dates were regressed against diel prey densities (Appendix 9). No significant relationship between predator and prey seine densities (nocturnal only or all samples combined) could be found for striped bass, bluefish, or weakfish. Daylight predator samples occurred so infrequently that meaningful regressions analysis was not possible.

DISCUSSION

This paper describes, for the first time, the fish fauna of a meso to polyhaline Chesapeake Bay littoral zone containing a typical conglomerate of different habitats. Its congruently operated duel gear approach provided samples of species across a wide range of sizes but its methods and materials had potential limitations.

Potential Limitations

In order to properly interpret data collected, the limitations of the study's methods and materials must be addressed. The first concern is a lack of sample site replication. Unfortunately, it is very difficult given economic constraints to achieve temporal and spatial diversity within a single study. The scale of the project's field methods prohibited the multiple site and short-term repetition of collections typical of most sampling efforts. Repetition and multiple sites were sacrificed in favor of large catches diverse enough to adequately determine assemblage structure and species-specific abundance for a large area temporally.

Estimates of assemblage structure and abundance in both gears may show species specific bias due to gear restrictions and sampling techniques, diel stage and/or tide of deployment, a fish's behavioral and physiological characteristics, and/or species-specific patterns of distribution. Any bias in assemblage structure and abundance would be included in mass and abundance density estimates.

Although the combined efforts of prey seine and haul-seine provided a large number of species in a wide range of sizes suggesting that a comprehensive quantification of finfish assemblage on various trophic levels was attained, gear restrictions due to material and methods exist that need to be discussed.

The prey seine was always operated during the day at mid-tide in the same location. It was deployed from shore, swept across the sample site, and landed back onshore. Prey seine length limited the depth of water fished and reduced mesh limited the speed at which the gear could be operated. Unequal distribution of species on a diel or tidal stage and/or across depths reached by gear may affect assemblage structure. There is significant evidence to suggest that diel fish distributions in the shallows vary for both predator and prey species (Hobson, 1965; Adams, 1976 b, c; Heck and Orth, 1980; Kleypes and Dean, 1983; Brooks, 1985; Weisberg et al., 1981; Ryer, 1987, Roundtree and Able, 1993, Sogard and Able, 1994; Cicchetti, 1998; Negelkerken et al., 2000). In vegetated North Carolina littoral zones fish biomass has been found to double at night (Adams, 1976 a, b). In response to this increased nocturnal predation pressure some prey species alter their nocturnal distribution (Cicchetti, 1998; Roundtree and Able, 1993). Feeding forays into the shallows by transient predators are known to follow tidal influxes (Cicchetti, 1998) and diel stages (Lascara, 1981; Grecay and Targett, 1996a; Spraker and Austin, 1997; Buckel and

Conover, 1997). Gut fullness of fishes (Rozas and LaSalle, 1990; Archambault and Feller, 1991; Roundtree and Able, 1992b), prawns (Mayer, 1985), and portunid crabs (Ryer, 1987; Fitz and Weigert, 1991) is greater on high or ebbing tide than during low or flooding tides.

Baltz et al. (1993) found that small fish abundance decreased as depth increased. The highest densities of organisms found in Louisiana's salt marshes are found within 3 m of the water's edge (Peterson and Turner, 1994) and community structure varies according to depth (Rakocinski et al, 1992). If a given species remained in shallow water as the tide ebbed and was, therefore, concentrated on the waters edge (Edgar and Shaw, 1995a), the assemblage structure and density estimates would reflect this disproportionate abundance. However, if a given species chose to concentrate in tidal creeks or other habitats (Butner and Bayard, 1960) not included in this study's prey seine beach sample site, reported abundance might be negatively biased. Given these examples, caution should be taken if this study's prey seine densities are applied to estimate prey biomass in other littoral zones. Habitat type and depth should be closely matched to sampled site's to minimize differences due to nekton's unequal distributed across habitats and/or depths (Cicchetti, 1998; Edgar and Shaw 1995a).

The haul-seine was large enough and was deployed in such a manner that it largely prevented escape by fishes too large to fit through its mesh from the study site after deployment. It was operated during both day and night to provide diel comparisons. Its consistent deployment on high tide, however, did not provide comparisons between tides. The mesh size of the haul-seine was a potential limitation. The legally required mesh size of 70mm was adopted to permit small fishes a means of escape. For example, conditioned (covered with antifoulant) 70mm (3") mesh retains spot >213 mm, releases 50% of fish 212mm and all fish < 211mm. Similarly, it retains all weakfish over 313mm and retains 50% of the 258mm size class (Myers, 1973). The size released is a function of girth at a given length, a species-specific characteristic that can show considerable variability. Haul-seine catch composition likely underestimates the abundance of YOY and smaller species found at depth due to its mesh size. Haul-seine density estimates for smaller fishes and YOY should, therefore, be regarded as being conservative.

Abundance estimates in both gears likely misrepresent fish that are inherently poorly sampled by seines due to their behavior or physiology. Species-specific abundance estimates may also be confounded by tactics like diel schooling (Evans, 1993). Adult and juvenile summer flounder were seasonally available in the study site and were collected in both gears but determining the abundance or biomass density estimates was problematic for both gears. No small flounder were available for prey seine analysis and no tagged fish were recaptured in the haul-seine. Lack of recapture suggests that seines may be an inefficient way of sampling flatfish. Seines may pass over the fish as it remains sedentary, or body shape may allow small depressions in the benthic topography to serve as sanctuary from gear. With such an unclear picture of flatfish gear interaction, gear efficiencies for flatfish species were estimated in both gears.

Inaccuracy in gear efficiency determination is inherently included in density estimations. Unfortunately, species-specific gear efficiencies could not be attained for many of the species captured. Inability to determine recapture rates and thus gear efficiency estimates affects several species density estimates in both gears. The recapture rate applied to summer and winter flounder captured in the prey seine was 57%. This was the average recapture rate as determined by mummichog, the dominant finfish species. This probably underestimates the abundance of YOY flounder in the site. A gear efficiency of 20% was applied to summer flounder, Atlantic thread herring, menhaden, oyster toadfish, striped mullet, striped burrfish, northern puffer, butterfish, and spadefish capture in the haul-seine. This percent was based on the fact that most of these species captured were small and were either gilled in the seine or only retained in the last two small mesh sections of net that enclosed about 20% of the site's area. A gear efficiency of 90% was applied to the cownose and other ray categories because the specimens captured were large and their active pelagic escape response to the gear actually increased likelihood of capture because escape attempts were easily recognized and prevented. The category other rays was not include in the catch results due to species confusion and relatively insignificant biomass.

Gear Efficiency

Comparisons

The complexities of gear efficiency need to be better understood to improve our application of scientific data obtained using various methods. Seine gear efficiencies have been found to vary significantly with species and size class (Weinstein and Davis, 1980, Allen et al. 1992). Using rotenone after seining through tidal creek sections isolated with block nets Weinstein and Davis (1980) found that seines (n=11) collected 46% of available fishes with a species-specific range of 20-84%. In size specific work large fishes (40-100mm) were recaptured at a rate of 81% and 75% of small (25-40mm) fishes were recaptured. Interestingly, for the three most abundant species sampled seines captured a greater percentage of individuals (61-78%) than rotenone alone (30-58). A similar study by Allen et al. (1992) repeated the seine then rotenone methodology in a tidal pool also isolated by blocker seines at low tide. They made a series of 15 consecutive hauls and found that on average 30% (range: 23-53%) of fishes were captured on the first haul. Species-specific effectiveness varied considerably (range:7-91%) for the six most abundant species. Estimated finfish recapture rates in this study ranged from 41-84% and collected an average of 57% of available species (based on Nov. data). The average percentage of available fishes collected in this study (57%) is higher than that found by Weinstein and Davis (1980) (46%) and Allen et al. (1992) (30%). Differences in assemblage structure will affect range of recapture (Rozas and Minello, 1997). Species specific comparisons between average recapture may provide a better source for comparisons:

striped killifish 53% and mummichog 27% (Allen et al., 1992) compared to this study's 69% and 44%.

This study's prey seine efficiency results suggest that efficiencies of active gear are affected by various factors including but not limited to species behavior, environmental temperature, habitat and/or experimental method (Rozas and Minello, 1997). Species-specific predator avoidance behaviors may affect recapture rates in seines. Schooling pelagic (*Brevoortia tyrannus*) species seeking safety in numbers have been found to be more susceptible to seine capture due to schooling than demersal species (*Fundulus heteroclitus*) that hide in benthic structure (Allen et al., 1992).

Higher recapture rates in this study may be due to benthic habitat, water temperature, and/or recapture rate determination method differences. Allen et al. (1992) operated their seine across an uneven hard bottom covered with shell but no benthic structure existed in this study's prey seine site. Mummichog recapture rates suggest that water temperature can play a significant role. Fish are cold blooded and their metabolism is integrally linked to environmental conditions (Beamish, 1970). Metabolic environmental dependence is reflected in swimming speed (Olla and Studholme, 1971; Stewart et al., 1983) that results in variable gear escape capabilities at varied temperatures. Water temperatures can affect different species in very different ways depending upon their physiological tolerances. Increasing water temperatures have a significantly different effect on spot and striped mullet seine capture than on mummichog. Spot and mullet capture rates increased at higher temperatures, hypothetically because the fishes were approaching physiological limits that reduced escape ability (Allen et al., 1992). Warm water temperatures were found to reduce mummichog capture rates in Allen et al. (1992) and this study. Year round analysis by Allen et al. (1992) conducted in South Carolina included much warmer water temperatures than this study. Environmental differences between studies likely effected average recapture rates.

In addition, none of the fishes included in the average recapture rate determined by Allen et al. (1992) or Weinstein and Davis (1980) were previously captured, held, or tagged. Weinstein and Davis (1980) size specific study did include fish which were subjected to the stresses related to capture and retention (75-81%) was much higher than that determined in average recapture rates trials based on rotenone application to previously seined waters. Increased rates of recapture with previously retained fishes suggest that recapture rate may be affected by the physical stress associated with capture and retention. Fishes whose escape is slowed by physical stress (Allen et al., 1992) or tagging will likely have higher recapture rates. Caudally clipped mummichog in this study showed an increased recapture rate verses dorsally clipped fish under identical environmental conditions. Differences among species, size-classes, and environmental variables must be taken into account when seine collection data are interpreted (Allen et al., 1992; Rozas and Minello, 1997). Variability in factors can be so large that collection efficiencies should be performed at least once during each season (Allen et al., 1992).

The reduced size of the prey seine made repetitive operation relatively easy. Repetitive operations provided sufficient data for statistical analysis of various methodological and environmental factors that potentially affected gear efficiency estimates. Haul-seine gear was selected because it is a large gear capable of isolating a vast littoral area and it has historically been used in the Bay's shallows to provide large varied catches of fishes including piscivores of interest (Hilldebrand and Shroeder, 1928). Its large size and method of operation, however, prohibited repetitive operations. No analyses of any large-scale seines were available in the literature. The limited results of this studies efficiency experiments suggest that the gear inherits some of the same limitations evidenced by analysis of its smaller counterpart.

Species-specific haul-seine gear efficiencies varied widely from 0-100%. Finding similar variation between large and small seine gears suggests that seines in general have highly variable species-specific recapture rates. Gear efficiency experiments were only conducted twice (at very similar water temperatures) and only two species (Atlantic croaker and summer flounder) were repetitively examined. Fifty percent of the croaker tagged were recaptured in both trials (n=169 and n=20) and no flounder (n=2 and n=2) were ever recaptured. A complete lack of deviation in recapture rate between trials in both species suggests that the gear, when operated in a consistent manner in a single site, can provide reasonably precise fish capture. It also highlights weaknesses of the gear: efficiency is species specific and highly variable and the gear may be an inadequate means of sampling some species especially if their density is low. No striped bass, bluefish, or weakfish were tagged because striped bass did not occur during trials and bluefish and weakfish did not survive tagging and recapture stresses required. Red drum and sandbar shark were the only large piscivores tagged (see appendix 1). The recovery rate of red drum (57%) suggests that size and swimming speed does not significantly alter the gear's efficiency.

Prey Seine

Gear Comparisons

Comparisons of the finfish assemblage structure collected by this study's prey seine and other methods also used around Goodwin Island show considerable variability due to gear. Flume net (Ayers, 1995), drop ring enclosure (Cicchetti, 1998), and seine experiments conducted in similar habitats retained very different fishes. Extensive flume net (Ayers, 1995) collections retained 11 species, drop ring (Cicchetti, 1998) experiments sampled 24, and this study's reduced number of seine samples collected 32. Flume net and drop ring enclosure methods recorded very low numbers of YOY commercially important species and contained no striped bass, bluefish, or weakfish though these fish are known to be present in the area (Chao and Musick, 1977; Cicchetti, 1998). The flume net included only 2 (summer flounder, spot) and drop ring methods collected 4 (spot, speckled trout, American eel, red drum) respectively.

Both Ayers (1995) and Chichetti (1998) recorded resident mummichog as the biomass and numeric dominant finfish. Mummichog appeared as the forth most abundant finfish in this study following Atlantic silverside, silver perch, and bay anchovy. Spot was the biomass dominant finfish. Sample area and method likely explains some of the assemblage and diversity differences. Ayers (1995) sampled 22.5 m^2 in tidal creek habitats. Cicchetti (1998) sampled 8.75 m^2 in the same muddy-sand *ruppia* / *zostera* habitat as this study but the area sampled in this study was greater than an order of magnitude larger (352 m^2). Small sample areas are not as well suited for sampling species with low densities because the area sampled may be less than the mean area occupied by a single individual. Enclosure traps like those employed in both these studies tend to underestimate densities of larger more mobile fishes (Jacobsen and Kushlan, 1987) and this weakness is augmented as sample area is reduced.

No scientific use of a large-scale seine was available in the literature. Comparisons between much smaller scientific seine studies and haul-seine samples are not reasonable due to vast differences in gear morphology, however, several large scaled studies using gill nets and trawl sampling methods were conducted at the mouth of the York River near the study site. Vast differences in scale with regard to area sampled, habitat composition, and methods exist however, and these may complicate and limit meaningful comparisons between studies (Livingston, 1987). Comparison between assemblage structure evidenced in this study and that reported by the Virginia commercial haul-seine industry can be made which bolster the viability of this study's haul-seine data set with regard to its use as a fishery independent reference (Appendix 10).

Orth and Heck (1980) conducted a 14-month trawl survey across *zostera* beds at three different sites during the day and found 48 finfish species. Catches across sites were dominated by spot, northern pipefish, bay anchovy, silver perch, and Atlantic silversides (in decreasing abundance order). Heck and Thoman (1984) conducted a similar study for 24 months in the same location but collected during day and night and included sand sites and gill net collection methods. They collected 42 species of fishes. Spot again dominated collections at vegetated sites followed by Northern pipefish, and silver perch. In sand sites fourspine sticklebacks, Inland silver sides, and Atlantic silverside followed spot.

Thirty-two species were collected in 7 months by the prey seine in this study. The prey seine site contained a sand bottom with sparse stands of widgeon grass. It was surrounded by various littoral habitats including eelgrass beds. The dominant species collected was Atlantic silversides followed by silver perch, bay anchovy, mummichog, striped killifish, and rainwater killifish. Orth and Heck (1980) collected 22 species and Heck and Thoman (1984) 20 species in common with this study. There were 8 species collected by the prey seine that were not collected by either trawl study, most of these occurred in low numbers in seine collections. There were several notable exceptions, however. Striped killifish and rainwater killifish were common in the seine samples but were noticeably absent from the Heck and Thoman study (1984). Depth distribution, habitat type, study length, and gear differences likely played a role in the reduced diversity and abundance discrepancies provide in this study.

The combination of seines employed in this study collected 52 finfish species in 8 months. The haul-seine collected 31 fish species 11 of which were also collected by the prey seine but the size composition of these species varied tremendously between gears (Appendix 3, and 6). The dominant species collected in the haul-seine was gizzard shad followed by croaker, spot, striped bass, bluefish and weakfish. Orth and Heck (1980) collected 14 species in common with the haul-seine. Trawls conducted by Heck and Thoman (1984) collected 15 species in common with the haul-seine. Additional gill net work supplied 4 additional species most notably larger elasmobranch species (cownose ray and sandbar shark) not reported in Orth and Heck (1980). Interestingly, 8 of the 17 species not collect by Orth and Heck (1980) and 7 of the 12 species not collected by Heck and Thoman (1984) are recreationally and/or commercially exploited species. Surprisingly, the most abundant species in haul-seine samples (gizzard shad) did not appear in either study's trawl or gill net collections and no weakfish were collected in trawl or daylight samples (Orth and Heck, 1980; Heck and Thoman, 1984).

Previous studies illustrate that gear selection affects species composition and size structure (Van Den Avyle et al., 1995; Knieb, 1997). Though a flume and seine net in Louisiana collected the same number of species (29), assemblage structure varied most likely due to habitat and seasonal differences (Peterson and Turner, 1994). Congruent gear comparisons between weir and seine samples in three different subtidal marsh creeks in New Jersey found differences between gears with seines providing the best characterization of dominant fauna (Roundtree and Able, 1992a). Combined efforts collected 64 fish total, 57 were collected in the weir and the rest in the seine. The combined results of these studies suggest that multiple gear methodologies can supply more accurate estimates of species diversity.

The dual seine approach used in this study supplied greater icthyofaunal diversity than previous works in the same area in a shorter period of time. Large differences in size distributions and species composition between gears stress the need to properly scale collection methods to targeted species and size class. Recognition of the effect of scale on species composition and size distribution suggests that data supplied by small-scale approaches alone may be inadequate with regard to provision of data necessary to guide fisheries management. Such findings heighten the need for fishery independent operation of commercial gears in order to establish more accurate estimates of bycatch, catch structure, and ecological impacts of gear operation.

Density Comparisons

In order to compare densities of small fishes collected by Ayers (1995) using flume nets, Cicchetti (1998) using drop rings, and this study's prey seine finfish density estimates from June to October (Table 2.3) were pooled. All comparisons were made between samples collected in open embayments in comparative depth strata from around Goodwin Island therefore surrounding habitat composition was similar. Ayers (1995) estimated fish density to be 1.5 m $^{-2}$ (exposed sites) and Cicchetti (1998) estimated fish density to be 2.4 m^{-2} (site three corresponding to Ayers). The estimated ichthyofaunal density in this study was 1.3 m$^{-2.}$ Comparisons suggests that this study's prey seine methods provide estimates that are comparable with those of Ayers and are likely conservative. No published density estimates of larger fish like those collected in the haul-seine could be found for the Chesapeake.

Species Composition

Fish assemblage structure in the Chesapeake Bay is inherently affected by season (water temperature). Catch data for both gears showed high seasonal variability in assemblage structure, biomass, and number due to immigration and emigration of transient fishes. Statistical analyses of correlations between Margalef's diversity index and water temperature were not significant for either. Though direct correlations did not mathematically exist, assemblage composition was reduced in the spring and fall and highest in late summer early fall in both gears.

Greatest prey seine diversity structure occurred in late summer through early fall in conjunction with largest biomass. Lowest abundance, biomass, and diversity were sampled in early and late fall in conjunction with the lowest water temperatures sampled. Peak abundance occurred in late July (marked by a peak in Margalef's index) primarily due to the arrival of YOY silver perch. Significant use of the site by YOY spot was also evident. YOY red drum, spotted trout, summer flounder, American eel, striped bass, black drum, spadefish, winter flounder, and sheephead (order of decreasing abundance) were also taken but in greatly reduced numbers. Blue crab was the biomass and numerical dominant species captured in the prey seine. This dominance supports the findings of previous investigators that vegetated littoral zones contain a large crustacean biomass and play a key role in production of this and other crustaceans.

Haul-seine assemblage structure was most diverse in the late summer and early fall as well. YOY spot, summer flounder, black drum, sandbar shark and bluefish (order of decreasing abundance) were collected in haul-seine samples despite the gear's larger mesh, which likely allowed passage of most small fishes. Increased fall diversity was likely due to immigration of YOY who had grown large enough to be retained in the gear and a few warm water transients. Lowest biomass and number occurred in early spring before water temperatures warmed. In late fall, striped bass immigrating into the flats kept haul-seine sample size and biomass large even though prey seine biomass and assemblage diversity was rapidly declining.

Sciaenids, among the most abundant large finfishes in the sample area (Massman, 1962; Colvocoresses, 1975; Markle, 1976), generally enter the York River starting in April and leave by December with peak abundance occurring in shoal areas in July (Chao and Musick, 1977). The pattern of sciaenid abundance evident in this study reflected that documented, including a peak in July (Hildebrand and Shroeder, 1928; Chao and Musick, 1977; McBride and Conover, 1992; Murdy et al., 1997).

The most surprising find of the study and possibly the most important with regard to export of energy from the system by a transient fish was the overwhelming and previously unquantified abundance and biomass of gizzard shad in the littoral zone. This species was the biomass and numeric dominant. Its biomass and number far exceeded that of all sciaenids combined. The biomass of these fish was so consistently large that the species may play a significant role in the bioenergetics of the system. Interestingly, little is known about the species trophic dynamics in saline systems and thus its trophic position and ecological niche are unclear. The species is well studied in fresh water where it often provides a rapid energetic linkage between trophic levels and substantially benefits large piscivores. Limnological investigations have shown the gizzard shad to be a highly efficient omnivorous filter feeder capable of filtering large quantities of water and thus effecting various predator and prey populations in different ways (Drenner et al., 1982). Its omnivorous habitats allow it to seemingly benefits from increasingly eutrophic conditions where it can occur in large abundances. From its omnivorous intermediate position, these fish can regulate food webs through a complex series of predation and competition interactions (Dettmers and Whal, 1999). In eutrophic systems, the species can enhance phytoplankton from both the bottom up and top down. Preferential selection for herbivorous zooplankton (DeMelo et al., 1992) can strongly enhance phytoplankton biomass and set the species in direct resource competition with young upper level fishes. Trophic resource competition can be so intense that the year class strength of upper level competitors is affected (Yako et al., 1996; Gu et al., 1996). Once zooplankton biomass is fished down, the gizzard shad can trophically decouple and remain abundant by switching to a diet of detritus (Lamarra 1975, Brabrand et al., 1990). While feeding on this diet, excretions provide a new source of dissolved nutrients readily assimilated by the phytoplankton community (Lamarra 1975, Brabrand et al., 1990). The effect of the shad's omnivorous habits is increasingly pronounced with augmented eutrophication (Drenner et al., 1996). In addition, the low N: P ratio of shad excretion may further alter the primary producer's community structure by favoring cyanobacteria (Schaus et al., 1997).

The biomass and abundance of shad found in this study's site is consistently so large that resource competition may be occurring that could compromise recruitment of other competing prey and/or predatory species (Yako et al., 1996; Gu et al., 1996). Trophic competition with gizzard shad over zooplankton is generally considered strongest at early life stages (Dettmers and Stein, 1992, 1996; Shepherd and Mills, 1996) and the Chesapeake's littoral zones provide nurseries to many YOY fishes that are ecologically, commercially, and recreationally important (Chao and Musick, 1977; Murdy et al., 1997).

The fact that it is the larger gizzard shad that inhabit the meso to polyhaline littoral zones of the Bay increases the likelihood that the fish maybe having a significant ecological affect because though conflicting literature exist as to which age classes of shad choose which food sources feeding success increases with size (Michaletz, 1996). Given the Bay's eutrophic state and trophic importance of zooplankton to economically important fishes, future studies should be done to describe and quantify this species' trophic dynamics and bioenergetic role. The urgency and importance of this work is augmented by the fact that gizzard shad are highly fecund, grow quickly, and thus rapidly escape top-down control by predators. Isotope analysis of gizzard shad gut seasonally in various Chesapeake Bay habitats within different riverine systems would significantly improve our understanding of the trophic niche these fishes fill and provide dietary comparisons with YOY fishes with which these fish may be competing.

Striped bass, bluefish and weakfish

Striped bass, bluefish, and weakfish were by far the most plentiful piscivores. Piscivore abundance showed an obvious nocturnal bias. Nocturnal preferences may be the result of extremely high daytime water temperatures in summer (Hampton et al., 1988), a greater nocturnal abundance of prey fishes and crustaceans found by other investigators in the area, which may be important prey items (Orth and Heck, 1980; Heck and Orth, 1980; Heck and Thoman, 1984), and/or avian predator avoidance. Day night trawl comparisons (Heck and Thoman, 1984) in the littoral zone near the sample site show higher daytime abundances of potential fish prey species in vegetated habitats (spot, silver perch, bay anchovy, Atlantic silverside). Abundances of the same species over sandy substrate varied with species. Spot had higher nocturnal abundance while silver perch remained unchanged. Atlantic silversides and bay anchovy showed marked abundance declines over such bottom at night. Consistently higher daylight abundances in these fishes may be due to schooling behavior or predator avoidance. Crustacean abundance (blue crab, grass shrimp spp, crangon) in both sand and vegetated habitats increased significantly at night. Unfortunately, trawls only captured one piscivore (summer flounder) in large enough numbers (n=320) to make diel comparisons and it occurred in both habitat types in much greater abundance at night. Diurnal avian predation by osprey (*Pandion haliaetus*), brown pelicans (*Pelecanus occidentalis*) and great blue heron (*Ardea heodias*) (general order of decreasing abundance) was at times intense during haul-seine operations. This predation was seasonal and intensified as fish to area ratio was increased during harvest. No nocturnal avian predation was observed.

Due to the reduced number of daytime samples and the greatly reduced piscivore abundances evidenced in samples, the discussions of general abundance and age structure are based primarily on fish gathered nocturnally.

Striped bass showed an increased abundance in cooler water temperatures and older fish showed patterns of documented migration. As waters warmed, a trend of declining striped bass abundance, size and age occurred. Bioenergetic studies by Hartman and Brandt (1995b) demonstrate that smaller bass are metabolically better suited to handle warm water temperatures and are able to maintain a positive scope for growth in temperature that far exceed the physiological thresholds placed on larger fish. Physiological limitations in warmer water offer a reasonable explanation for the decline in average size and age evidenced as waters warmed in this study and the resulting dominance of age 1 fish in warmer months. This hypothesis also offers an explanation for the complete lack of bass collected in the warmest months. Though small striped bass have a much greater tolerance of higher water temperatures than their larger cousins. For striped bass temperature for maximal growth declines with fish size while no ontonogenic differences in thermal optima for bluefish or weakfish was found (Hartman and Brandt, 1995b). Greatly varied physiological limitations likely lead to different survival strategies and trophic resource use. Adult striped bass have a thermal tolerance of 6-27C° (Merriman, 1941) but prefer temperatures of 18-25C° (Coutant, 1985). Temperature preferences have been found to motive migrations to more suitable condition in fresh water reservoir and riverine populations (Cheek et al., 1985; Bjorgo et al., 2000) and have been offered as an explanation for coastal migration patterns of the species (DeVries, 1982; Coutant, 1986; Schaffler et al. 2002). The largest striped bass sample size and mass collected in this study occurred in October congruent with a drastic drop in littoral temperature.

Dissolved oxygen also affects bass distribution (Schaffler et al., 2002). Anoxia has been observed in the Chesapeake since the 1930's (Newcombe and Horne, 1938) but it has become more wide spread and longer lasting in recent times (Flemer et al., 1983; Secor et al., 1998). Bass will select the coolest water available with a dissolved oxygen concentration greater than 2.5 mg/L (Crance, 1984; Matthew et al. 1989). If dissolved oxygen level is depleted in cooler waters bass will occupy temperatures warmer than those in its preferred range (Farquhar and Gutreuter, 1989; Zale et al. 1990). Predicted warming trends, increased alteration of stream flows, and increased hypoxia are predicted to further restrict striped bass habitat suitability in the Chesapeake in coming years (Coutant, 1990). If bass are forced to occupy warmer water habitats in order to attain desired oxygen concentrations bioenergetic models (Hartman and Brandt, 1995b) suggest that growth will be negatively affected. If bass populations continue to expand and trophically important prey providing habitats continue to degrade, bass may become limited by trophic resources. Hartman and Brandt's (1995d) work in the oligotrophic portion of the Bay suggests that this phenomenon is already occurring. Clearly, there is a need to further investigate this species physiology at specific life stages in order to improve our understanding of its tolerances and limitations. Numerous local and regional studies must be linked to provide a coastal perspective and investigations linking population health to the habitats that provide the prey-base upon which the population depends must continue (Hartman and Margraf, 2003).

Bluefish and weakfish are physiologically better suited for warm waters conditions. Their specific growth rates continue to increase at temperatures far above those that would limit or negatively affect bass growth. Bluefish and weakfish catches did not show marked decline in abundance with increasing water temperatures. Bluefish abundance, biomass and average age showed a minor peak in early spring. These highpoints could have been due to continued early season cohesion of immigrating schools. Weakfish abundance and biomass generally increased until it peaked in early fall. Bluefish were the youngest piscivores collected on average. No bluefish older than 2 were sampled and age 1 were dominant. Weakfish age breadth (1-8) was second to that of striped bass. Early spring (May) and fall (Sept.) samples contained the largest diversity of age classes and oldest fish. Age diversity at these times suggests that weakfish of vastly different age classes form schools in order to migrate together. Early fall (October 10, 2001) samples evidenced drastic reductions in bluefish abundance. Weakfish numbers showed an even more marked decline. Population contractions occurred congruently with a decline in prey density, a sharp drop in water temperature, and a large influx of striped bass. Bluefish and weakfish have considerably higher optimal growth temperatures (20 and 20.3C° respectively vs. 15C° for striped bass)(Hartman and Brandt, 1995b). Littoral temperatures in early October (16C°) were well below optimal for bluefish and weakfish but very close to that of striped bass. Striped bass are also a known predator of weakfish in this portion of the Chesapeake (Walter and Austin, 2003).

Assemblage structure in all piscivore species showed a shift towards smaller, younger fish during mid-summer. No size dependent thermal optima, like that which exist in striped bass, have thus far not been found for bluefish and weakfish (Hartman and Brandt, 1995b) so motivation for size reductions is unclear. Smaller fish may be more prevalent in littoral zones due to the assemblage structure of prey resources provided. Littoral zone vegetations are known to be rich in invertebrate prey and in general the contribution of invertebrates to the diets of striped bass, bluefish and weakfish decreases with fish size (Hartman and Brandt, 1995a). A significant dietary reliance on crustaceans is well established for young striped bass (Gardiner and Hoff, 1982; Hartman and Brandt, 1995a). Bluefish and weakfish diets in a Chesapeake Bay littoral zone contained a much larger quantity of crustacean prey (Lascara, 1981) than that reported for fishes sampled from other habitats (Hartman and Brandt, 1995a, Baird and Ulanowitz, 1989). A recent synthesis of striped bass dietary analysis along the Atlantic coast (Walter et al. 2003) suggests that fish diet may be far more elastic and dependent upon habitat prey provision than previous works have suggested (Hartman and Brandt, 1995a,d).

Diversity and predator and prey density correlations

Statistical examination of the Margalef's diversity indexes formed for each gear showed that no significant correlation existed between the diversity of species sampled in the prey seine and that collected in the haul-seine. Attempts to find statistically significant correlations between prey density (abundance summed across species) and predator density (abundance of striped bass, bluefish and weakfish) were also unsuccessful.

There are various methodological reasons why relationships between seine samples may not have been found. The seines used were of vastly different dimensions. Turbidity has been found to have a significant effect on juvenile fishes' distribution (Blaber and Blaber, 1980) and escape reaction to active gear (Phil and Rosenberg, 1982) and environmental temperature seems to have a species-specific effect on gear efficiency. How these variables affected each species in each gear is unclear, but due to the extremely large differences in scale and species collected may have resulted in significant variability. Species-specific efficiency estimates in each gear may have been too variable to provide adequate estimates for comparison.

Prey seine samples were consistently collected during daylight and the majority of haul-seine samples were nocturnal. Diel cycle can significantly effect the distribution of nekton species (Adams, 1976a; Boynton et al., 1981, Kleypes and Dean, 1983; Brooks, 1985; Roundtree and Able, 1993; Sogard and Able, 1994). Distribution of the same species may vary based on specific characteristics like size (Sogard and Able, 1994; Clark et al. 2003). Size is important because it directly affects vulnerability to predation. The evidence supporting the importance of relative body size to predator success is unequivocal (Juanes and Conover, 1994a; Paradis et al. 1996; Rice et al., 1997; Scharf et al. 1998; Lundvall et al., 1999). The importance of size however may vary between piscivores species specifically. Striped bass and weakfish ingest their prey whole so prey items must be of the appropriate size to be vulnerable to predation. The bluefish is equipped with sharp teeth that make it capable of taking bite size pieces from prey normally too large to be swallowed. This alternative method may increase the size range of potential prey (Scharf et al, 1998). Prey size ranges were not taken into account in prey density estimates.

In addition to the distribution and gear restrictions mentioned above, comparison between predator and prey abundances may have been influenced by differences in prey vulnerability that occurred during the study. The complexity of intertidal and subtidal floral habitats was not fixed. Salt marsh continued to grow throughout the study period. Macroalgea moved freely through the system affected by both wind and tide. Eelgrass normally experiences maximum growth from April to July, followed by massive leaf loss from July to September, and a short regrowth period in early fall and winter (Orth and Moore, 1986). Shifting SAV (Olney and Boehlert, 1998), marsh grass (Currin et al., 1984; Cicchetti, 1998), and macroalgea (Coen, 1979; Heck and Thoman, 1981) densities provided varied degrees of prey vulnerability to predation. If piscivores are assumed to be opportunistic then vulnerability becomes the controlling factor. Prey vulnerability can be viewed as the product of prey's susceptibility to attack, the encounter rate (some function of prey density and cover) and capture success rate (size) (Greene, 1986; Bailey and Houde, 1989; Scharf et al., 2003). Prey susceptibility was assumed to be the same for all species. Cover and prey size were not considered in density comparisons between predator and prey. In analysis, prey density was assumed to be a reasonable proxy for prey vulnerability. This approach was likely an over simplification of the factors influencing predator and prey density dynamics. Future work would be greatly aided by increased information on congruent predator stomach content to aid in identification of potential prey items and sizes. Influential environmental data including turbidity and seasonal alterations in habitat structure should be included. A single collection method that sufficiently samples both predator and prey simultaneously in a site with reduced habitat complexity would also be preferred.

Management Implications

Fisheries scientists will continue to be faced with an increased demand for management decisions to be based on an ecosystem perspective (Brandt et al., 1992). Ecological modeling is being pushed towards forecasting for management (Clark et al. 2002; Ludwig et al. 2001) a capacity that fisheries management has been operating in for years. This shift in emphasis is in part due to recognition that disturbances in part of the system can have cascading effects throughout the system's trophic structure (Carpenter, 1988) and local density-dependent (biological) processes can significantly affect production dynamics at the population and ecosystem level (Kareiva and Andersen, 1988; Possingham and Roughgarden, 1990). Spatial variability in predator and prey interactions is well recognized (Brandt et al., 1992). System-wide averages of predator and prey abundances that do not incorporate effects of spatial variation are likely inadequate for improving understanding of production dynamics or predator and prey interactions (Brandt et al. 1992). Applying an ecosystem approach will require a better understanding of the effects of habitat on species interactions and population dynamics.

To understand the mechanisms regulating production dynamics in aquatic systems the biological function of various biological and physical structures must be evaluated (Carpenter, 1988; Powell, 1989). An improved understanding of the prey diversity and refuge functions provided in specific habitats is of practical value to fisheries management because habitat loss is one of the leading reasons for diminishing species diversity (Minns, 1999). Loss of prey diversity can increase dietary overlap (competition) between predators (Setzer et al. 1980; Mercer, 1983) and restrict predator production (Pope, 1979). In addition, loss of biodiversity may have potentially negative consequences on the Earth's ecosystem functions (Sculze and Monney, 1993). It is important to the effective evaluation of the ecological effects coastal habitat modifications have had on fisheries resources and the design of alteration s to minimize value losses (Boesch and Turner, 1984). The Magnuson-Stevens Act of 1996 recognizes the importance of spatial variability to production and the scale-dependent linkages between biological function and biological and physical structure in its focussed on identification of Essential Fish Habitat (EFH). Application of the EFH concept applies directly to littoral zones and the various habitats they contain.

Since habitats are inherently spatial it is important to understand the diversity differences provided in various habitats. Habitat specific spatial processes are particularly important in fisheries models and will have implications for the design of marine reserves (Thorrold et al., 2001). Optimal forage theory assumes that natural selection will favor the development of feeding preferences that will maximize energetic gain per time, therefore, feeding behavior and thus habitat choice are based on optimizing energy gain (Enlem, 1966). Establishing species-specific finfish densities within a given habitat provides a means of comparing biological function between habitats based on species diversity and abundance. An important tenet of these comparisons is that greater densities indicate improved quality or preferred habitats (Zimmerman and Minello, 1984; Sogard and Able, 1991; Baltz et al, 1993). Establishing a given fish's density is the first step in establishing scale-dependent linkages between biological function and the biological and physical structures that regulate a habitat's contributions to that stock. The central premise of the Habitat Suitability Index (HIS) (FWS, 1980a, 1980b, 1981; Terrel and Carpenter, 1997), developed by the U.S. Fish and Wildlife Service as a means of linking fish stocks to habitat, is that the "value" of an area of "habitat" is determined by its carrying capacity as it relates to density-dependent population regulation (FWS 1981). Establishing densities of known piscivore prey, therefore, allows for estimation of a habitat's potential to produce such fishes.

Littoral zones contain the habitats most often negatively impacted by human expansion and are known to be highly productive at the secondary level (Odum, 1971). On such habitat, oyster reefs, have received a great deal of attention in the Chesapeake Bay because they were once a significant littoral habitat and significant efforts have been made to restore them. Today, the bay's littoral zones contain very few oysters. Examination of created reefs in the Piankatank River found 32 fish species, including species commonly consumed by striped bass and bluefish (Harding and Mann, 1999, 2001, 2003). The increased habitat complexity found on these reefs was credited with augmentation of transient fish size and abundance (Harding and Mann, 2001). Greater finfish and prey diversity (Hartman and Brandt, 1995a) presumably make a site more attractive as a foraging arena (Harding and Mann, 2001a,b) and this basic comparisons between diversity and abundance for the bases of the 52 species of finfish were collected in this study's littoral zone, but the sample site included an increased diversity and complexity of habitat. Comparisons between oyster reefs and littoral habitats containing a diversity of structurally complex habitats suggest that controlling shoreline development and increasing efforts to revegetate altered subtidal and intertidal habitats is potentially more valuable as an enhancement tool for finfishes than simply restoring oyster reefs.

Seasonally high predator and prey diversity and abundances suggests that the complex and overlapping nature of habitats typically found in the bay's littoral zones may offer improved trophic benefits to highly mobile upper level fishes in comparisons to the individual habitats that make up these zones. The implications this concept has on establishing relevant criteria to aid in the identification of essential fish habitat and the ecological significance of lower level biodiversity on the production of upper level fishes needs to be investigated further.

CHAPTER 3. DIETARY ANALYSIS OF WEAKFISH, BLUEFISH AND STRIPED BASS IN VEGETATED CHESAPEAKE BAY LITTORAL ZONE

ABSTRACT

Striped bass (*Morone saxatilis*), bluefish (*Pomatomus saltatrix*), and weakfish (*Cynoscion regalis*) are dominant piscivores in the Chesapeake Bay. This study investigated and compared the diets of these piscivores in a Chesapeake Bay littoral zone, which contained a diverse habitat composition including intertidal marshes, submerged aquatic vegetation, macroalgae beds, mud flats, and sand bars. Diets of all three species contained a much larger proportion of crustaceans than had been evidenced by most previous investigations. Annually blue crab dominated the diet of ages 1-3 striped bass and weakfish. Age 1 bluefish relied most heavily on *Paleamonetes* shrimp (28%). Other stomach content studies from vegetated Chesapeake littoral zones have also found a similar increase in importance in crustaceans in diets but have not found these invertebrates to dominate diet. Older weakfish (age 3 <), striped bass (age 4 ≤), and bluefish (age 2) diets consisted primarily of finfish in accordance with findings of most previous studies; however, finfish of a benthic origin were more prevalent. Also in agreement with most previous investigations the importance of clupeid prey increased with age across species. Diet content and diversity varied across age classes seasonally often reflecting increased prey abundance suggesting that these piscivores are opportunistic feeders. Weakfish across age classes often contain both pelagic and benthic prey congruently. This finding may suggest that the species employed more elastic

feeding strategies than competing piscivores. In general trophic ecology of piscivores reflected decreased dependence on benthic prey with age and an increased consumption pelagic prey in the fall. Dietary overlap was significant (>50%) between bluefish and weakfish from May through September when age classes were pooled. When examined age specifically overlaps between species were evenly distributed between piscivores and overlap was generally short-term in duration. Greatest overlap between age classes within a species occurred in striped bass. Consumption of secondary level benthic prey across species evidenced a trophic relay that rapidly transferred littoral energy to piscivores that in turn carried this production out of the system. This transfer may be an important conduit of piscivore production, which has not been previously described or taken into management considerations. The increased diet diversity evidenced by piscivores in littoral zones has implications with regard to the opportunistic nature of piscivore predation, essential fish habitat designation, and placement of marine reserves.

INTRODUCTION

Successful resource management requires a balance between the social and economic demands placed on a resource and the biological constraints that limit sustainable resource harvesting (Langton et al. 1996). Essential habitat limitation can potentially create thresholds that constrain population dynamics, range, and abundance (Gallaway et al. 1999; Collins et al. 2000; Doka, 2001; Loucks et al. 2003). The Magnuson-Stevens Fishery Conservation and Management Act of 1996 (hence forth Magnuson-Stevens) recognizes the importance of ecological alterations, the essential nature of some habitats and how the direct and indirect losses of these habitats have resulted in diminished capacity to support existing fishing levels (MCFCMA, 1996). In order to provide for maximum sustainable yields, high value habitats referred to as essential habitats by Magnuson–Stevens must be identified and species-specific requirements understood and quantified (NMFS, 2000). Linking production parameters and rates to habitat can help identify potential limits to productivity and thus define "essential habitats".

Diet studies of predatory fishes are the first step in determining the trophic pathways and quantifying the contributions that are essential to management of both predator and prey (Livingston, 1985). Spatially (habitat) specific energetic pathways need to be defined to establish trophic interactions and quantify their effect on growth, and hence, production of these species (Brandt et al., 1992). Striped bass

(*Morone saxatilis*), bluefish (*Pomatomus saltatrix*) and weakfish (*Cynoscion regalis*) inhabit most of the Atlantic's coastal waters and support valuable commercial and recreational fisheries throughout their range (Wilk, 1979; Setzler et al., 1980; Mercer, 1983; Mid-Atlantic Fishery Management Council, 1989; Hartman and Brandt, 1995 c; Richards and Rago, 1999). Like most commercially important inshore fish species along the Atlantic Coast of North America, these species rely on estuarine resources during many of their life history stages (McHugh 1967; Day et al., 1989) and, thus, may be affected by shifts in estuarine habitat composition and prey resource availability (Carpenter et al., 1985, 1987).

The dynamics of these species are of ecological interest not only because they span three families of fishes (*Moronidae, Pomatomidae,* and *Sciaenidae*) but also because they are often the top piscivorous predators in many estuarine systems (Chao and Musick, 1977; Friedland et al., 1988). As the principle apex predators, their dynamics and trophic impacts may alter the structure and function of lower levels in a top down manner (Carpenter et al., 1985, 1987) or, as Hartman and Brandt (1995d) suggest is currently the case in the Chesapeake piscivore production, may be limited by prey availability in a bottom up fashion (Carpenter et al., 1985, 1987). Because prey production is linked to the quantity and quality of suitable habitats, this hypothesis has obvious implications with regard to historic reductions in the coverage of vegetated littoral zones. Theoretically, highly mobile transient fishes can overcome short-term and/or small-scale prey species' reductions by emigration to other areas within an estuary. However, if long-term ecological alterations limit the resources available for forage species' production, cascading effects throughout the trophic architecture of the estuary could result (Carpenter et al., 1985; Posey and Hines, 1991).

All three species use the Bay's habitats as nurseries and feeding areas although estuarine residence time and bioenergetic benefits each gain from specific habitats may vary greatly (Lankford and Targett, 1997). Weakfish and bluefish immigrate into the Bay in the spring and emigrate in the fall (Chao and Musick, 1997). Anadromous striped bass have a much more complicated pattern. Some of the smaller and mostly male fish are residents, but the larger (>711mm TL) fish migrate into the Bay in the spring and fall (Chapman, 1987). All mature fish move into tidal freshwater tributaries in the spring to spawn (Chapoton and Sykes, 1961; Dorazio et al., 1994). After spawning, larger fish leave their offspring to mature in the Bay and migrate north along the coast where they spend the duration of summer. Migratory fish return to the Chesapeake in the fall to take advantage of trophic resources produced during the summer. Historic landing data and the preceding faunal survey evidence these patterns with a spring peak in March-April and a fall peak in October-November (Koo, 1970; Coutant, 1987; Walter et al. 2003b).

Previously, most studies of dietary composition have taken samples randomly using various gears from across habitat types (Chao and Musick, 1977; Lankford and Targett, 1994; Hartman and Brandt, 1995a). This is partially due to the difficulty in designing sampling methods that ensure stomach contents were obtained in the area of interest. Results from random sampling may provide useful comparative information on average growth and/or diet composition but tell nothing about habitat specific predator prey interactions or dependencies. The only published large-scale diet study examining striped bass, bluefish, and weakfish in the Chesapeake to date used a random sampling design within the northern portion of the Bay. The northern Bay's environment, including physiochemical properties and provision of habitat, is very different from the lower Bay (Murdy et al., 1997). Diet composition and habitat preferences within such different subsystems may vary considerably due to the resources each contains. In the northern bay menhaden (*Brevoortia tyrannus*), bay anchovy (*Anchoa mitchilli*), and spot (*Leiostamus xanthurus*) were found to account for 65-99% of the annual biomass consumed by striped bass, weakfish and bluefish, excluding age 0 striped bass that ate mostly invertebrates (Hartman, 1993, Hartman and Brandt, 1995 a).

A few habitat specific diet studies have been conducted and these studies reflect elastic diets that seem to suggest links between prey availability and stomach content but none have been for all three piscivores simultaneously in a Chesapeake Bay littoral zone. Striped bass sampled from salt marsh creeks in Delaware Bay contained mostly blue crabs (*Callinectes sapidus*), grass shrimp (*Palaemonetes vulgaris*), sand shrimp (*Cragnon septemspinosa*) and mummichog (*Fundulus heteroclitus*)(Tupper and Able, 2000; Nermerson and Able, 2003). Fishes from oyster reef habitats in the Chesapeake showed increased dependence on benthic reef related species (Harding and Mann, 2001; Harding and Mann, 2003). Lascara (1981) explored weakfish and bluefish diets in SAV beds along Vaucluse Shores on the Eastern Shore of the Chesapeake from April to November using gill nets and found that these shallows were primarily used nocturnally by weakfish. Only large bluefish were sampled but they were less influenced by diel cycles. Stomach content analysis within these zones and associated sand flats showed that diet of both species within grass beds was more varied and contained more crustaceans. An increased trophic importance of crustaceans has been found for most finfish species examined in grass beds (Adams, 1976; Brook, 1977; Edgar and Shaw, 1995b).

Local habitat specific density-dependent processes may significantly affect production dynamics at the population and ecosystem level (Brandt et al., 1992). Within the Bay, large-scale reductions in the coverage of vegetated littoral zones may have had cascading effects throughout the trophic architecture of the system (Carpenter et al. 1985; Posey and Hines, 1991). Seagrasses produce dense infaunal and epifaunal crustacean communities (Orth, 1977; Heck and Orth, 1980; Penry, 1982), prey organisms fundamental to the habitat's value to higher predators (Thayer et al., 1975; Heck and Thoman, 1984; Fredette et al., 1990; Lubbers et al., 1990; Cicchetti, 1998; Chao and Musick, 1977; Murdy et al., 1997) that in littoral zones in other estuarine systems have been found to form a vital trophic link between primary production and transient fishes (Brook, 1977; Edgar and Shaw, 1995 b). Habitat differences in prey biomass and availability alter trophic energy intake and affect predator condition linked to population biomass and reproductive effort (Lankford and Targett, 1994, 1997; Hartman and Brandt, 1995b, d; Grecay and Targett, 1996b). The effect that alterations in the Bay's littoral habitat composition have had on its ability to produce upper level fish biomass remains unclear. Although the predator-prey interactions that define energetic exchange within vegetated littoral zones at lower trophic levels have been well documented, many questions remain as to the quantity of biomass and how and when it is transferred to higher levels and ultimately out of the system (Kneib, 1997).

Bluefish catches within the Bay were very high in the 1970's when the striped bass population was at a historic low. Since striped bass recovery, bluefish catches within the Bay have drastically declined (VMRC). Biotic competitive interactions have been proposed as an explanation for observed opposite trends in landing data (Anonymous, 1998; Buckel and McKown, 2002). Concurrent ecological alterations in the bay's littoral habitat composition may offer an alternative explanation. SAV coverage of the bay's shallows was much more extensive in the 1970's (Orth and Novak, 1990). Alterations in habitat composition may have affected prey resource production and/or distribution and these alterations in turn unequally affected trophically dependent piscivorous species. Prey sizes for striped bass have been found to overlap with those of much smaller bluefish (Hartman and Brandt, 1995a; Hartman, 2000). If trophic overlap coincides with prey abundance (Lucena et al. 2000), it need not indicate competition. However, if prey abundance declines due to habitat alterations, previously nondetrimental amounts of overlap may, depending on the severity of overlap, result in competitive interactions (Setzler et al., 1980; Mercer, 1983), lower maximum sustainable yield (MSY) (Pope, 1979), or top-heavy systems that are easily upset by fishing pressures (Walters, University of British Columbia).

Although we recognize how productive these habitat types are at the primary and secondary levels (Wetzel and Penhale, 1983; Dennison et al., 1993), and the trophic reliance of adult piscivores on many of these lower level species (Thayer et al., 1975; Chao and Musick, 1977; Cicchetti, 1998), no large scale scientific study has been conducted to quantify and qualify these fishes' trophic dependence on littoral zone habitats. Most studies have concentrated on a single species, group of species, habitat type, and/or the smaller individuals easily attained using small gears. Such restricted methods have provided little information on habitat use by large predatory fishes that rapidly transit across overlapping shallow water habitats. Our understanding of community structure, abundance, and biomass of such predators in the shallows is, therefore, extremely limited (Peters and Cross, 1992).

Detailed food habitat studies are necessary to account for the temporal, spatial, and ontogenetic nature of trophic interactions that influence multi-species fisheries (Walters et al., 1999; Hallowed et al., 2000; Whipple et al., 2000). Temporal stomach content studies that simultaneously target competing predators within specific habitats are necessary to provide habitat dependent effects on diet content, overlap and consumption. Analysis of functional parameters such as growth, based on long term habitat specific diet studies, may be a useful way of examining habitat contributions (Engelmann, 1968) and provide a means of directly comparing habitats (Healey, 1972) thus aiding managers in identification of essential habitats.

To accurately assess dietary contributions to fish, data must be collected when feeding is occurring. Feeding forays into shallows by transient predatory fishes are known to follow tidal influxes (Cicchetti, 1998) when access to prey is maximized. Numerous investigators have also found that diel stage also affects predator abundance and stomach fullness (Lascara, 1981; Grecay and Targett, 1996a; Spraker and Austin, 1997; Buckel and Conover, 1997). Fish biomass doubles at night in North Carolinian vegetated littoral zones (Adams, 1976 a, c). Increased finfish abundance has also been found at night in Chesapeake Bay littoral zones (Orth and Heck, 1980). Increased predator feeding activity, reduced gear avoidance, and/or lower nocturnal temperatures may motivate diel differences (Adams, 1976c; Orth and Heck, 1980). One dominant prey species (*Menidia menidia*) has apparently even altered its nocturnal behavior by spreading across the marsh surface at high tide events to attain refuge from this increased nighttime predation pressure (Roundtree and Able, 1993; Cicchetti, 1998). Lascara (1981) who studied piscivore diel variances along the Eastern shore of the bay by comparing gill net samples found that diel effects were piscivore specific.

Choice of sampling gear depends on target species, fish size, and area of operation (Van Den Avyle et al., 1995). Active (e.g. seines, trawls, throw nets) and passive gears (e.g. fyke nets, traps, flume nets, and other enclosure devices) are both commonly used to sample small nekton species (Knieb, 1997). Active gears provide nearly instantaneous samples from fairly defined areas but can only be operated in open waters (Knieb, 1997) and can have low and variable catch efficiencies (Rozas and Minello, 1997) that are species specific (Allen et al., 1992). Consequently, in some situations enclosure devices are preferable (Rozas and Minello, 1997). However, even large enclosure devices underestimate the densities of large fishes (Jacobsen and Kushlan, 1987) and different species vary considerably in their susceptibility and are affected uniquely by trap design and a host of other factors (Sheaves, 1995). Previous flume net (Ayers, 1995) and drop ring enclosure (Cicchetti, 1998) devices deployed in the study area recorded very low numbers of transient piscivorous species and included no striped bass, bluefish, or weakfish, though these fish are known to be present in the area (Chao and Musick, 1977; Cicchetti, 1998).

Active gear have been found to provide more accurate estimates of food consumption than stationary devices because they sample both low-activity non-foraging, actively feeding fishes (Hayward et al., 1989) and large scale gear in general provides more accurate estimates of abundance, biomass, assemblage composition, and trophic consumption than small ones (Livingston, 1987). A comparison of six active gears (e.g. hydroacoustics, trawling, gillnetting, electrofishing, shoreline seining, and cove rotenone) found based on CPUE of shad in freshwater reservoir that no one gear was clearly superior (Van Den Avyle et al., 1995). Seines are commonly used for estuarine sampling of fishes. Large seines called haul-seines have been used to harvest commercial quantities of fishes in the bay since European colonization. A large haul-seine was employed in this study in order to prevent the research question from exceeding the dimensions of the ecological system sampled.

The low catch efficiencies, commonly associated with seines, were corrected for by minimizing the parameters that lead to inconsistent performance. Sample area and methodology were standardized to improve precision. A seine's performance is also integrally linked to the topography and structural aspects of the bottom across which it is swept. Selecting a single sample site that contained a benthic composition conducive to gear operation improved consistency. Standardizing operational procedures and personnel further minimized variance.

The objectives of this chapter are as follows: to identify and quantify both seasonally and annually the trophic resources benefiting upper level fishes in a typical vegetated mesohaline littoral zone habitat; to quantify diet composition; to examine the degree of dietary overlap between striped bass, bluefish and weakfish; and to determine the trophic pathways of these fishes while feeding in these shallow water habitats.

SITE, SAMPLING PERIODICITY, AND METHODS

Study Site

For a complete description of study site see chapter one and two.

Sampling Periodicity

A total of fourteen samples were taken from April to November 2001. Samples were collected twice monthly, except for November when only one sample was collected. In addition, gear failure compromised the nocturnal sample conducted in August. One daylight sample was collected every other month throughout the study period.

Methods

Field methods

A haul-seine was used as a sampling device in this study. The haul-seine is a large commercial gear traditionally used to harvest fishes from shallow water. It has provided and continues to provide large diverse catches of fishes in the Chesapeake.

The seine used for data collection in this study adhered to the regulations governing commercial haul-seine gear as set forth in the Laws of Virginia Relating to Marine Resources of the Commonwealth (1998). The net consisted of ten separate sections that, when tied together (lapped), created a single seine 914m (3000 ft) long. All sections were 3.04m (10 ft) tall with floats along the topline and leads along the bottom. The first 762m (2500 ft) of this seine consisted of five sections composed of 7.62cm (3 in) mesh. The last two shorter seines contained a reduced mesh of 5.08cm (2 in) in order to decrease gilling during the landing procedure. Catch was gradually forced into a small area by systematically pulling each section to shore and then removing it. Eventually, the catch was contained within a small circle created by the landing wings. A box containing a bottom (pocket) would then be tied between the terminal ends of the wings and a heavily weighted seine, called a wing, pulled across the area within the circle forcing the catch into the pocket.

Sometimes striped bass catches were too large to allow for total retention. In this case 50 fish or 10%, whichever number was larger, were selected randomly from the total catch and the remainder released. All bluefish and weakfish were retained. All harvested specimens were packed in ice aboard vessels to deter deterioration and transported to the lab.

Laboratory methods

Laboratory processing which included measuring fish length (+ or – 1.0mm total length, TL), weight (+ or – 0.1g wet weight after blotting) and removal of stomachs was conducted within 24 hours of collection. Stomachs were frozen immediately and stored for later analysis. This analysis included measuring full stomach weight (+ or – 0.1g wet weight after blotting), empty stomach weight (+ or – 0.1g wet weight after blotting) and examination, identification, numerical count, and mass measurements of stomach content based on species or prey group.

Prey groups

Weakfish with damaged guts (n=14) were not included in dietary analysis. All other stomachs, including empty stomachs, were included in analysis and statistics. Prey items were identified to lowest possible taxon whenever possible. Identification to species was not possible for all prey due to digestion and/or partial remains. Groups based on taxon were polycheate spp., clam spp., amphipod spp., isopod spp., mysid spp., *Crangon*, *Paleamonetes spp.*, *Panaeid* shrimp spp., and unknown juvenile shrimp species. Gobiesocids (goby spp.) and gobiids (skillet fish) were placed in separate groups. Anchovy spp. included bay and striped and silverside spp. included all atherinids. Pipefish spp. included all syngnathids. Groups were formed based on the assumption that the predator was not distinguishing between species while feeding and species occupy similar habitats and employ similar predator escape and avoidance tactics. In addition, species-specific identification was often complicated by digestion. Remaining prey items were identified by species.

Two conglomerate groups, unknown, principally consisting of crustacean parts, and unknown fish were also necessary. Submerged aquatic vegetation (SAV), macroalgae spp., shell, rocks, spartina spp., and fish scales also appeared in stomach content and are so labeled.

Data analysis

Cumulative Prey Curves

Cumulative prey curves were constructed based on cumulative diet across age classes for each piscivore in order to determine if sufficient samples were collected to adequately describe diets (Huturbia, 1973; Cailliet, 1977, 1979; Barry et al., 1996; Ferry and Cailliet, 1996; Cortes, 1997). Curves plot stomach number against the number of new prey types occurring in each stomach during each trial. Stomach order was randomly reordered 15 times in order to provide standard error bars. Graph included all stomachs sampled and all prey. An asymptote indicates the minimum number of stomachs required.

Diet Content

Traditionally, diet content studies include counts, frequency of occurrence, and mass or volume of prey items or categories (Hynes, 1950; Hyslop, 1980). All of these measures are useful in different ways in determining the importance of various prey. Numerical abundance elicits feeding behavior (MacDonald and Green, 1983), volume or weight measures reflect nutritional value (MacDonald and Green, 1983), and occurrence increases our knowledge of population-wide prey habits (Cailliet, 1977). One of the more widely used compound indices is the index of relative importance (IRI) (Pinkus et al., 1971; Cortes, 1997). IRI accounts for weight, numerical abundance, and frequency of occurrence in the gut of each predator species examined thus cancelling out some of the inherent biases of each individual component (Bigg and Perez, 1985). This index can therefore provide a useful tool for examining diet content (Pinkus et al., 1971; Manooch and Mason, 1983; Ruderhausen, 1994). The index is expressed as:

$$IRI = (\%N + \%W) * \%O$$

where,

% N = percent numerical count,
% W = percent weight (wet weight gm)
and % O = percent frequency of occurrence.

The strength of this index lies in its combination of terms and thus it's minimization of biases obvious in individual components (Bigg and Perez, 1985). The bias that can be incorporated into IRI is obvious if we examine one of its components. Percent O, the portion of stomachs containing a species or specific category of species, is a nonadditive index because several different prey items of the same species or individuals within a functional group can occur within a single stomach simultaneously. Summing across all stomachs and dividing by stomach number can result in > 100%. Percent IRI is more robust to changes in %O and therefore, provides a better standard for study comparisons (Cortes, 1997). It is calculated as:

$$\% \, IRI_i = 100 IRI_i / \sum_{i}^{n} IRI_i .$$

Previously mentioned methods of statistical analysis including gut fullness index (gm prey/gm predator, Hall et al. 1995) and mean stomach content weight (average gm wet weight of prey/predator, Elliot and Persson, 1978) were calculated for each age class of piscivore occurring in each sample. Age structure of piscivores was estimated based on length age regressions (Robillard et al., in prep.; Boboko et al. in prep.; Boboko et al., in prep.; See Appendix 11).

Trophic ecology

Nocturnal samples collected in the same month were combined to estimate monthly diet composition based on %W (wet weight). Diel samples were not included in trophic ecology analysis due to reduced size. Individual samples varied in age class structure as determined by age length equations (Appendix 11) and percentage of stomachs examined within each age class. When more than one sample containing a given age class was collected in a month, sample and prey specific wet weights were weighted by each sample's age specific abundance. This was done so that total prey specific weight (y^{α}, where α represents a specific prey) per sample could be estimated. Corrections followed the equation:

$$y^{\alpha} = (\text{gm prey}^{\alpha} * 100)/(\#\text{ examined}/\#\text{ sampled})$$

Corrected prey specific weights for each sample within a month were then added. The weight of all individual prey categories was summed and each category divided by that sum to calculate prey specific %W for the month. Monthly % W estimates provided age specific temporal comparisons of diet content.

In order to examine temporal shifts in the trophic pathways that benefited piscivores at each age in littoral zones, each month's prey assemblage was divided into benthic and pelagic prey items. The benthic prey group contained species or functional groups that acquire most of their trophic resources from benthic sources (e.g. spot, Atlantic croaker, gobies, polychaetes, shrimp, and crabs)(Darnell 1958, Homer and Boynton 1978). The pelagic group consisted of those that acquire their energy from predominantly pelagic sources. They are represented by species like anchovy spp., silverside spp., and menhaden (see Appendix 12 for details)(Jefferies, 1975; Homer and Boynton, 1978). Percent wet weight (%W) of all species or functional group belonging to each pathway was summed and graphed to compare contributions over time and between age classes. Only data based on age groups that consisted of at least three stomachs containing prey per age group were used.

Annual wet weight percentages for each age group of piscivore were also calculated to provide comparisons between age classes and species. Because age structure was dynamic and total sample size was not a consistent percentage of total catch, prey specific mean stomach content (S^{α}, gm^{α}/indiv.) was weighted by each samples proportional age specific abundance to attain a properly weighted prey specific mass by fish abundance at each age ($S^{\alpha T}$, gm^{α}/ total sample).

$$S^{\alpha T} = S^{\alpha}((\#\text{ age class/sample size})*\text{ total catch})$$

Corrected prey specific weights were summed and each prey categories mass divided by this sum to calculate categorical %W for the year. Actual number of fish sampled in each age category, total age specific sample size, and total caught for each species can be seen in appendix 13.

Dietary overlap

Diet overlap comparisons were made between age classes of piscivores at each sample date and between combined ages monthly by applying the overlap index of Schoener (1970) by month. The index is calculated as:

$$100(1-(.5*\Sigma\ |p_{x,i} - p_{y,i}|))$$

with $p_{x,i}$ and $p_{y,i}$ are the W% of prey category i in predator species x and y (Steele et al. 1995; Garrison and Link, 2000).

This index is a robust measure of diet similarity (Wallace, 1981) and was applied by Hartman and Brandt (1995a). Its use here provides a means of comparison with their diet results, determined in other Chesapeake Bay habitats. The index computes a percentage overlap from 0 to 100%; 0 representing no overlap and 100 signifying complete overlap. An index of ≥ 60 was chosen as the arbitrary boundary to identify significant levels of overlap and has been widely used in the past (Zaret and Rand, 1971; Mathur, 1977; Johnson, 1981; Johnson and Ringler, 1980; McCabe et al., 1983). Prey categories followed those described previously. Flora, nonliving matter, and unknowns were excluded.

RESULTS

Cumulative prey curves provide a means of visually determining whether sufficient samples were collected to adequately characterize diet diversity. Cumulative prey curves based on all stomachs combined as given in Fig. 3.1-3.3 indicated that adequate samples were obtained for all three predators. This is visually indicated by the asymptote in each graph, which shows that no new prey species are being discovered by continued stomach analysis. All Figures contain 15 random orders of stomach examination and appropriate standard errors.

Age Specific Diet Analysis

Piscivore abundance during daylight samples was greatly reduced compared to nocturnal samples. Abundance was so low that seasonal comparisons between diel samples were not possible. Diel diet analysis when available is presented. If no data is presented for a sample date then either all fish collected were empty or no fish were collected. Striped bass were captured in small numbers in diel samples on March 12th and October 30th 2001 but were not examined or included. Following sections contain age specific percent wet weight (%W) results for samples where stomach number met or exceeded 3.

Figure 3.1-3.3. Cumulative Prey Curves were constructed for striped bass, bluefish, and weakfish gut content analysis pooled across age classes in order to measure if sufficient samples had been collected to accurately assess dietary diversity of each species. As the following graphs illustrate all prey curves reached asymptotic stabilization.

Fig. 3.1. Striped Bass

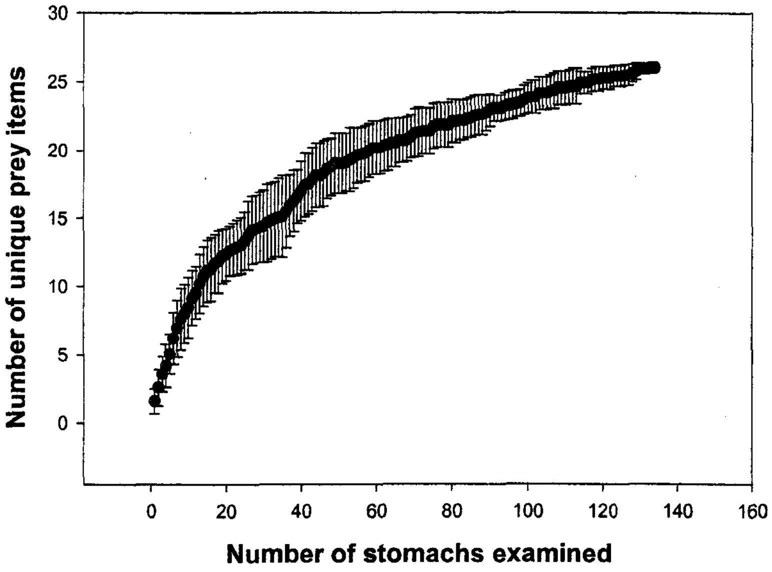


Fig. 3.2. Bluefish

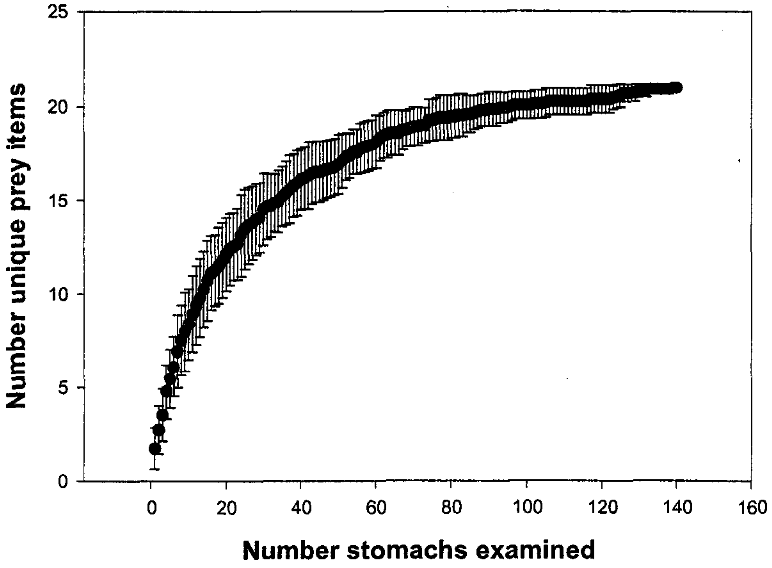
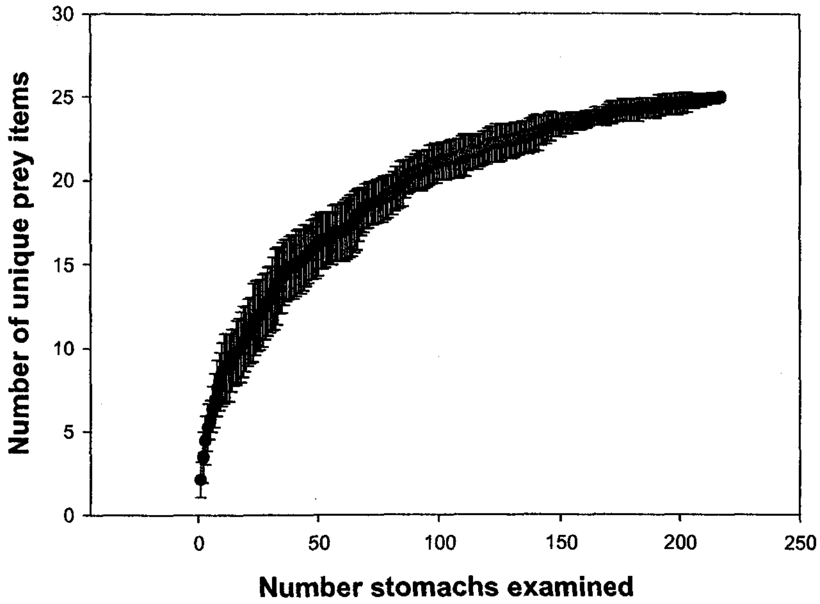


Fig. 3.3. Weakfish

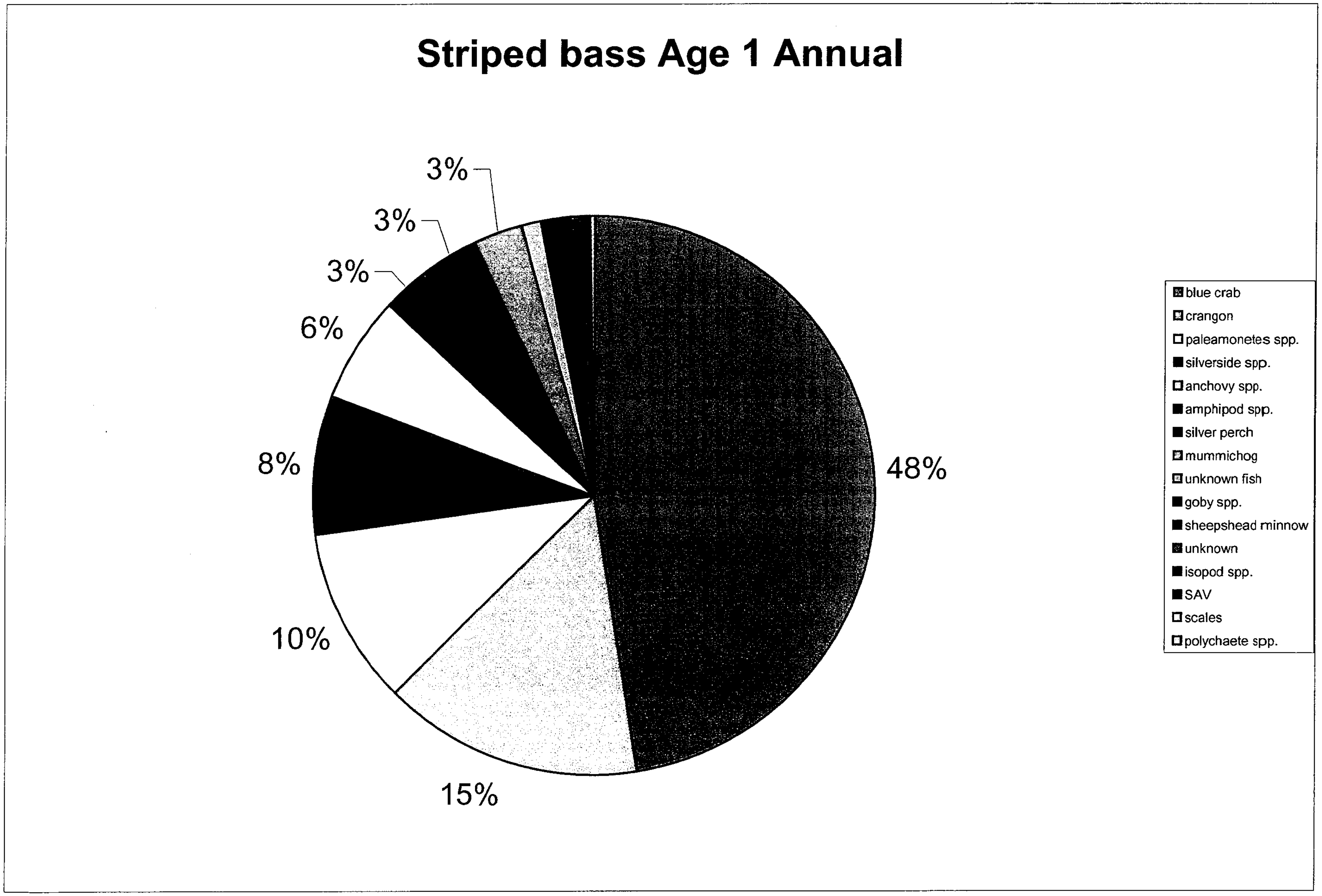


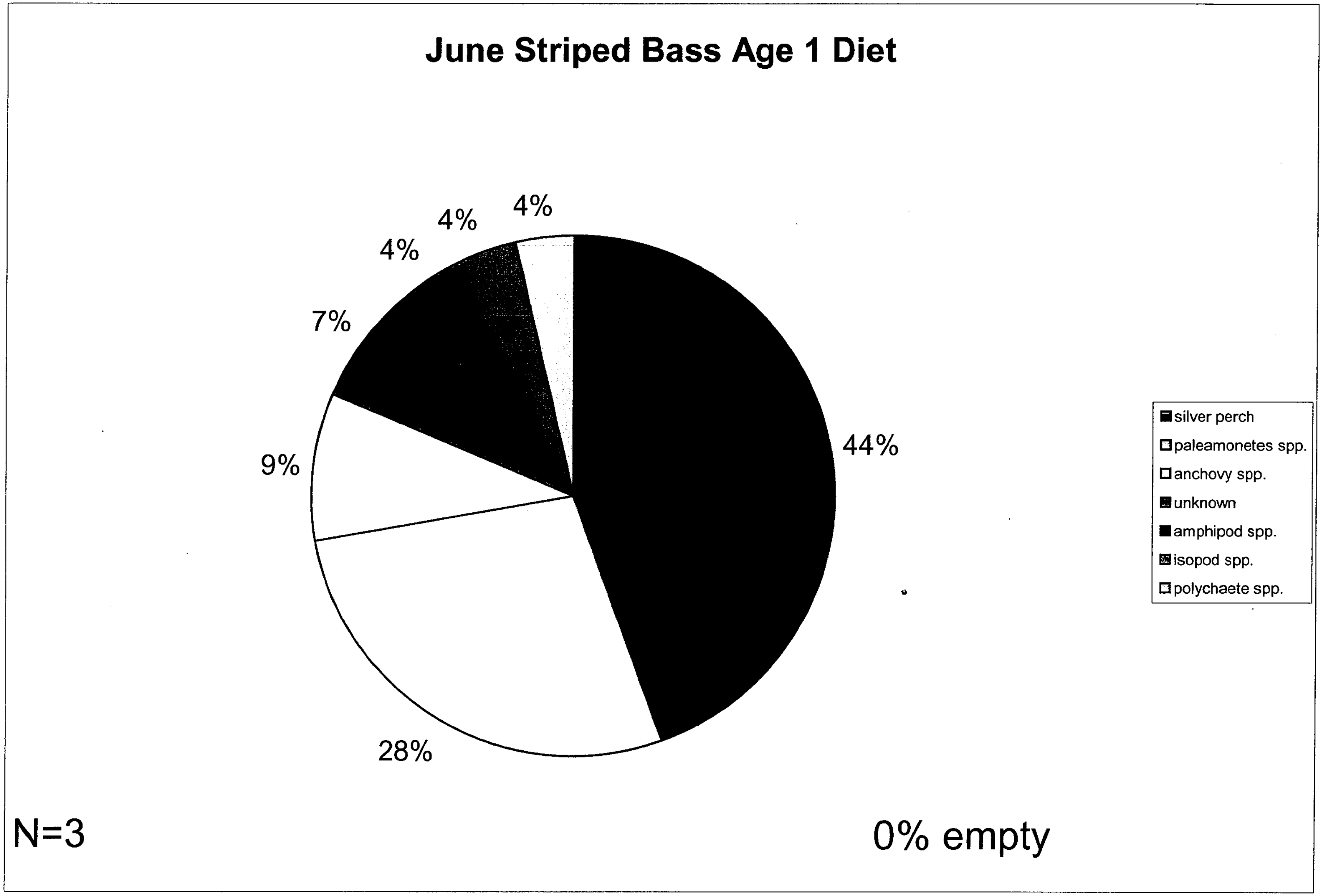
Ontenogenic stage and seasonal changes affected diets of striped bass, bluefish and weakfish. In general prey diversity decreased and relative mass of crustacean prey (W%) declined with age. Prey size and importance of clupeids increased with age. Sample, age and species specific results of indices are listed in Appendix 14.

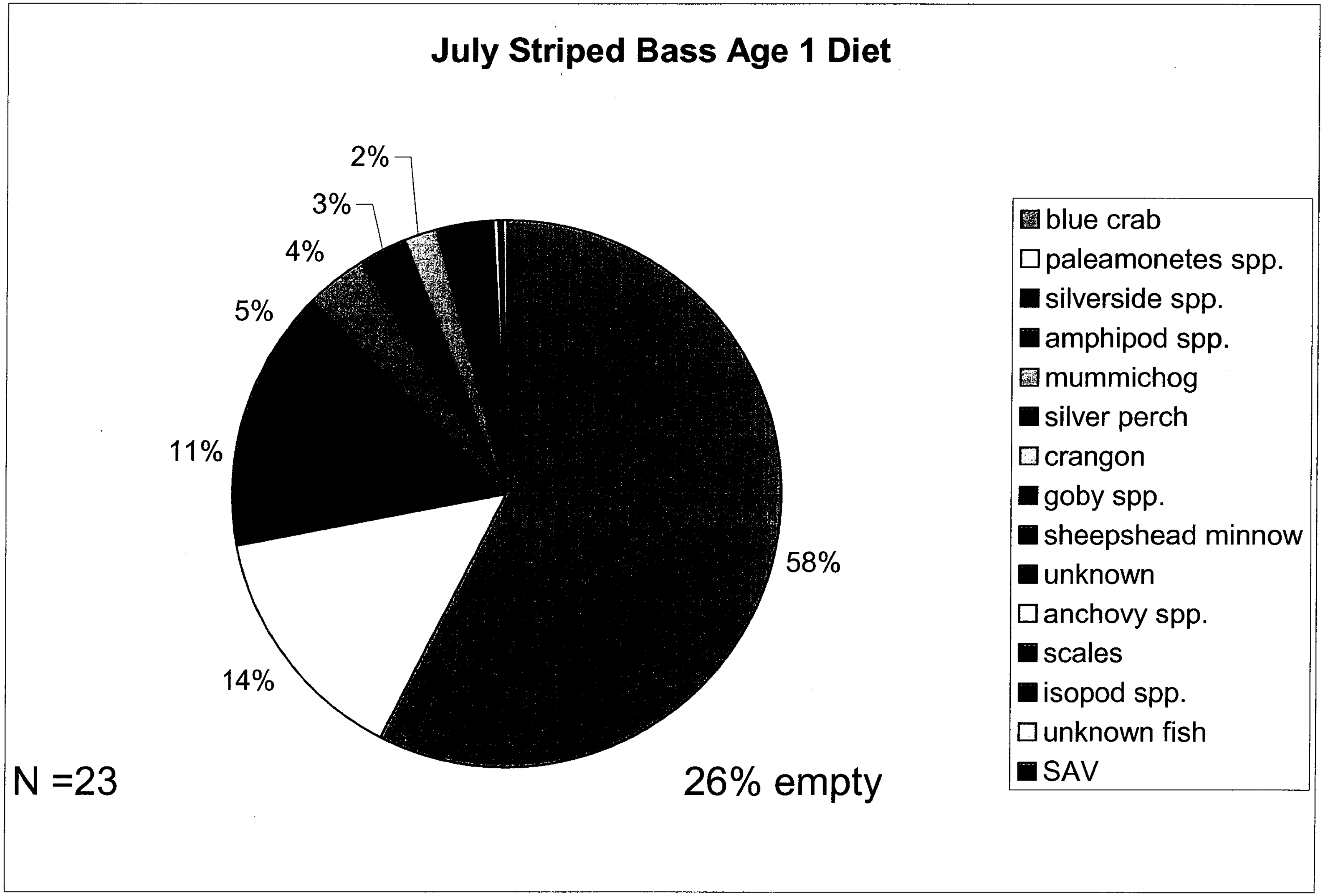
Striped bass

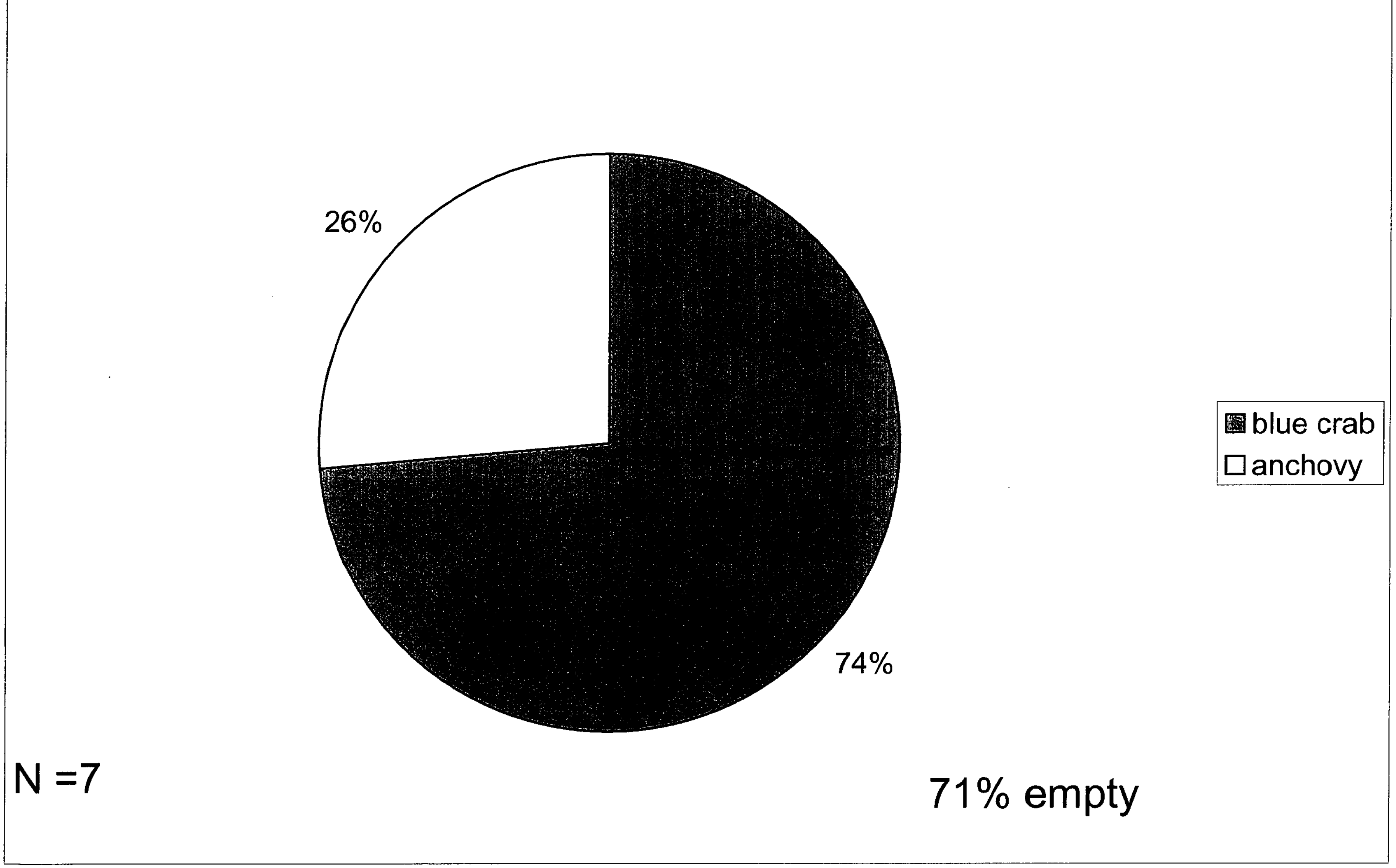
Annually, age 1 striped bass fed primarily on crustaceans: blue crabs (48%), crangon shrimp (15%), and paleamonetes spp. (10%). Smaller crustaceans were consumed in a reduced percentage (Amphipod spp. 3% and isopod <1%). The most important finfish were silverside spp. (8%), anchovy spp. (6%), silver perch (3%), and mummichog (3%)(Fig. 3.4). Sixty-eight percent of fish examined contained only benthic prey, 19% contained only pelagic and 13% contained both. Diets that combined both benthic and pelagic prey most often consisted of anchovy spp. and/or silverside spp. and paleamonetes shrimp. A small number of age 1 striped bass were present (n=5) in May but unfortunately these fish were not analyzed. June age 1abundance was also low (n=3). Diet was dominated by silver perch (44%), paleamonetes shrimp (28%) and anchovy spp. (9%)(Fig. 3.5). Small crustaceans also contributed (amphipod and isopod 4% each). July abundance was much improved and prey consumed during this month (n=15) was the most diverse of the study period. The mass dominant was blue crab (58%) followed by paleamonetes spp. (14%), and silverside spp. (11%). Amphipod and isopod spp. contributed

Figure 3.4-3.8. The figures that follow contain pie charts of age1 striped bass annually then monthly. Monthly figures are presented in order collected.

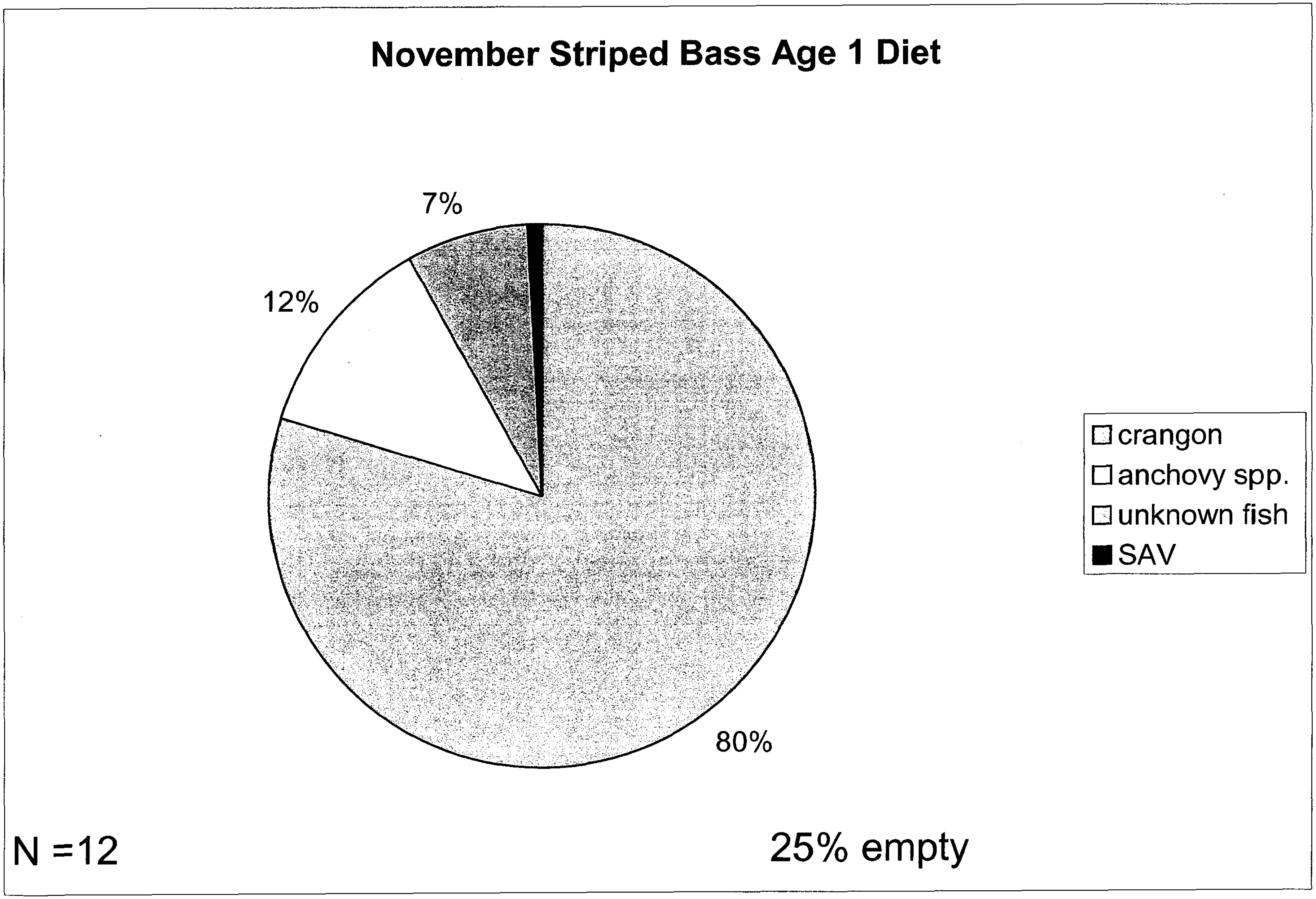

Striped bass Age 1 Annual
48%
15%
10%
8%
6%
3%
3%
3%
blue crab
crangon
paleamonetes spp.
silverside spp.
anchovy spp.
amphipod spp.
silver perch
mummichog
unknown fish
goby spp.
sheepshead minnow
unknown
isopod spp.
SAV
scales
polychaete spp.


June Striped Bass Age 1 Diet
4%
4%
4%
7%
44%
9%
28%
silver perch
paleamonetes spp.
anchovy spp.
unknown
amphipod spp.
isopod spp.
polychaete spp.
N=3
0% empty


July Striped Bass Age 1 Diet
2%
3%
4%
5%
11%
14%
58%
N =23
26% empty
blue crab
paleamonetes spp.
silverside spp.
amphipod spp.
mummichog
silver perch
crangon
goby spp.
sheepshead minnow
unknown
anchovy spp.
scales
isopod spp.
unknown fish
SAV



October Striped Bass Age 1 Diet



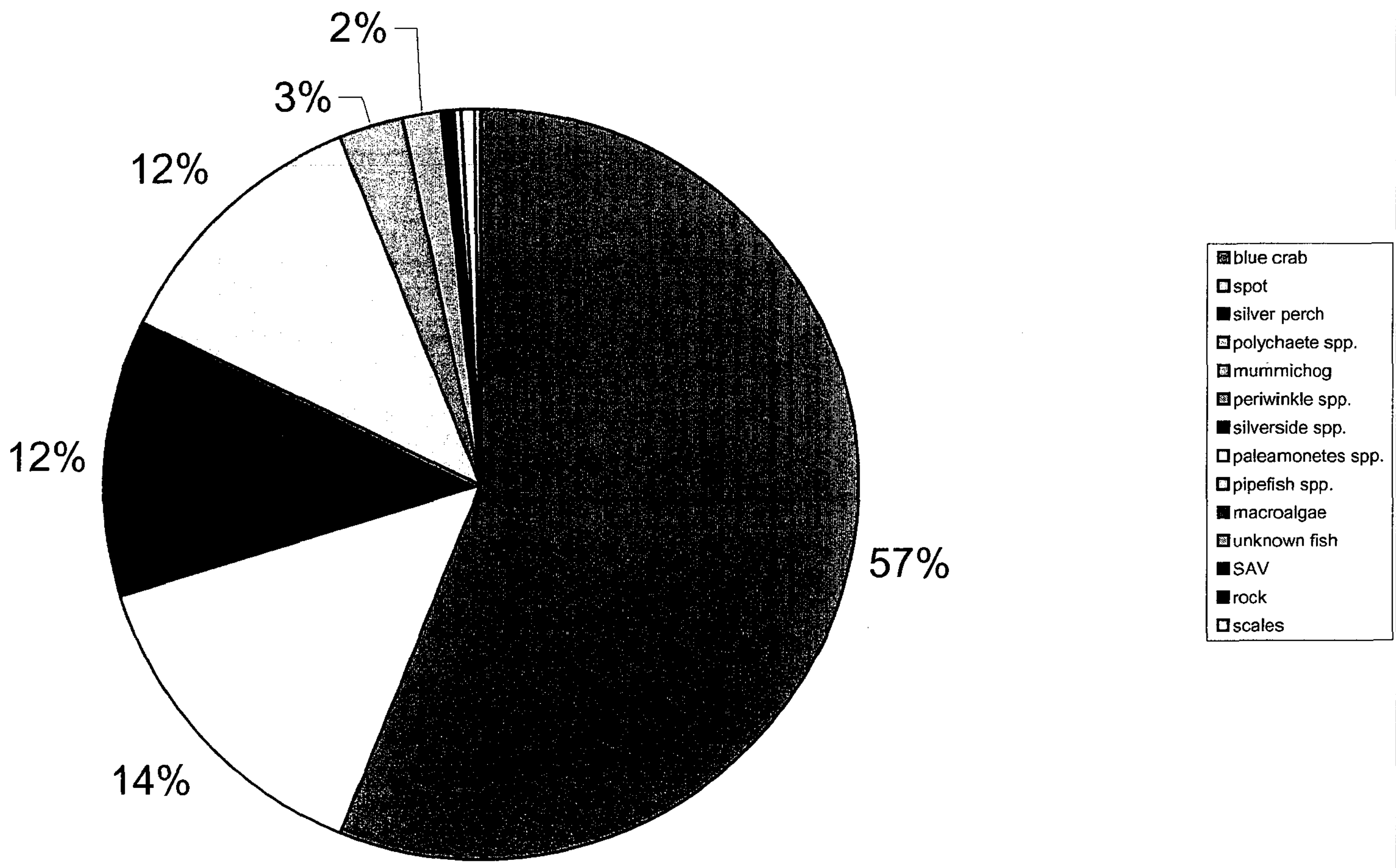
November Striped Bass Age 1 Diet

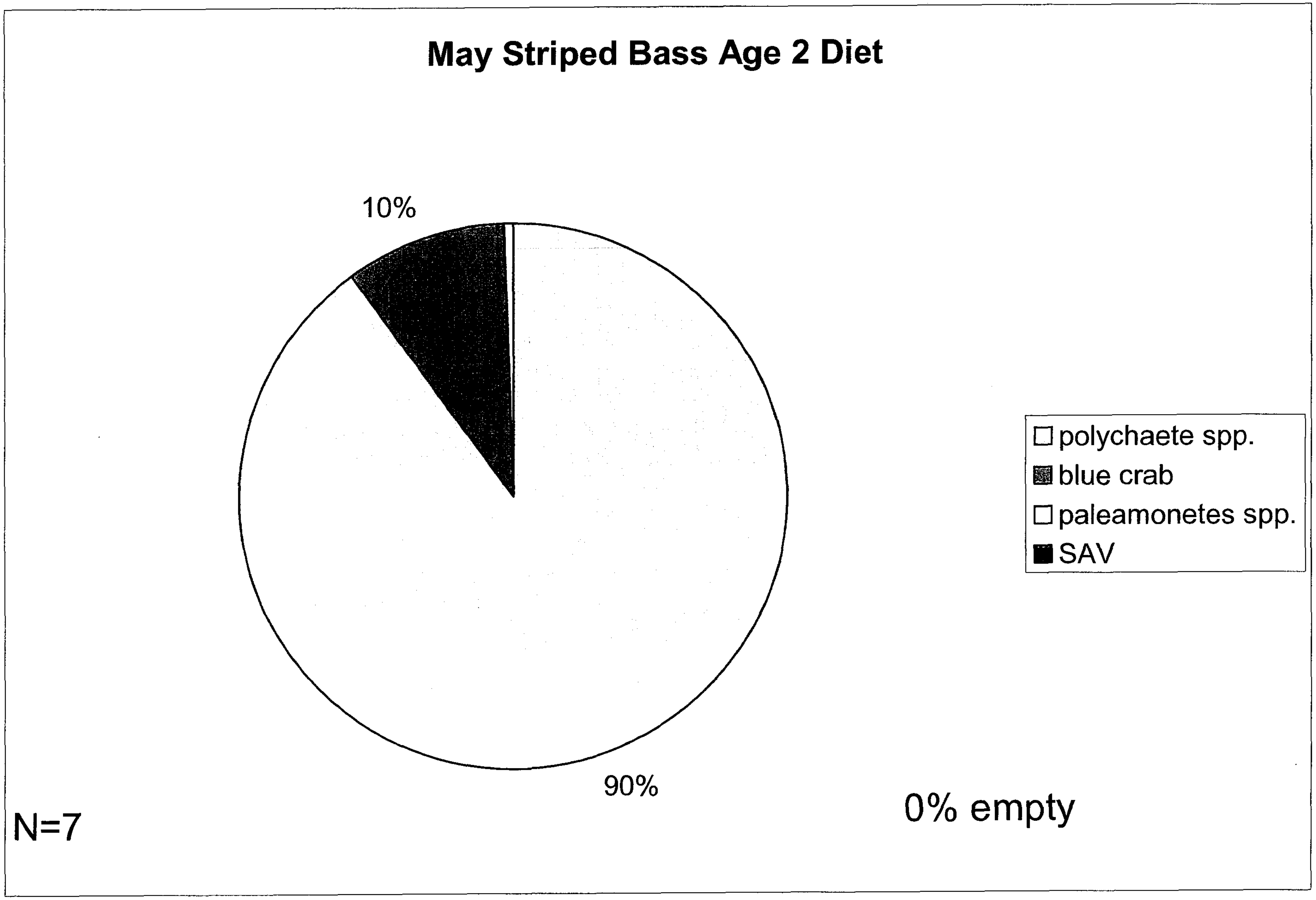
approximately 6% (Fig. 3.6). Age 1 fish were not sampled again in large enough numbers to provide month specific data until October. Fall diet showed less prey diversity than that in mid summer. October stomachs contained only two items (blue crab 74% and anchovy spp.) and the percentage of empty stomachs peaked at 71% (Fig. 3.7). November diet also only contained two identifiable prey items: crangon (80%) and anchovy spp (12%)(Fig. 3.8). Silverside spp. constituted a larger mass in mid-summer and anchovy spp. mass was greater in the fall.

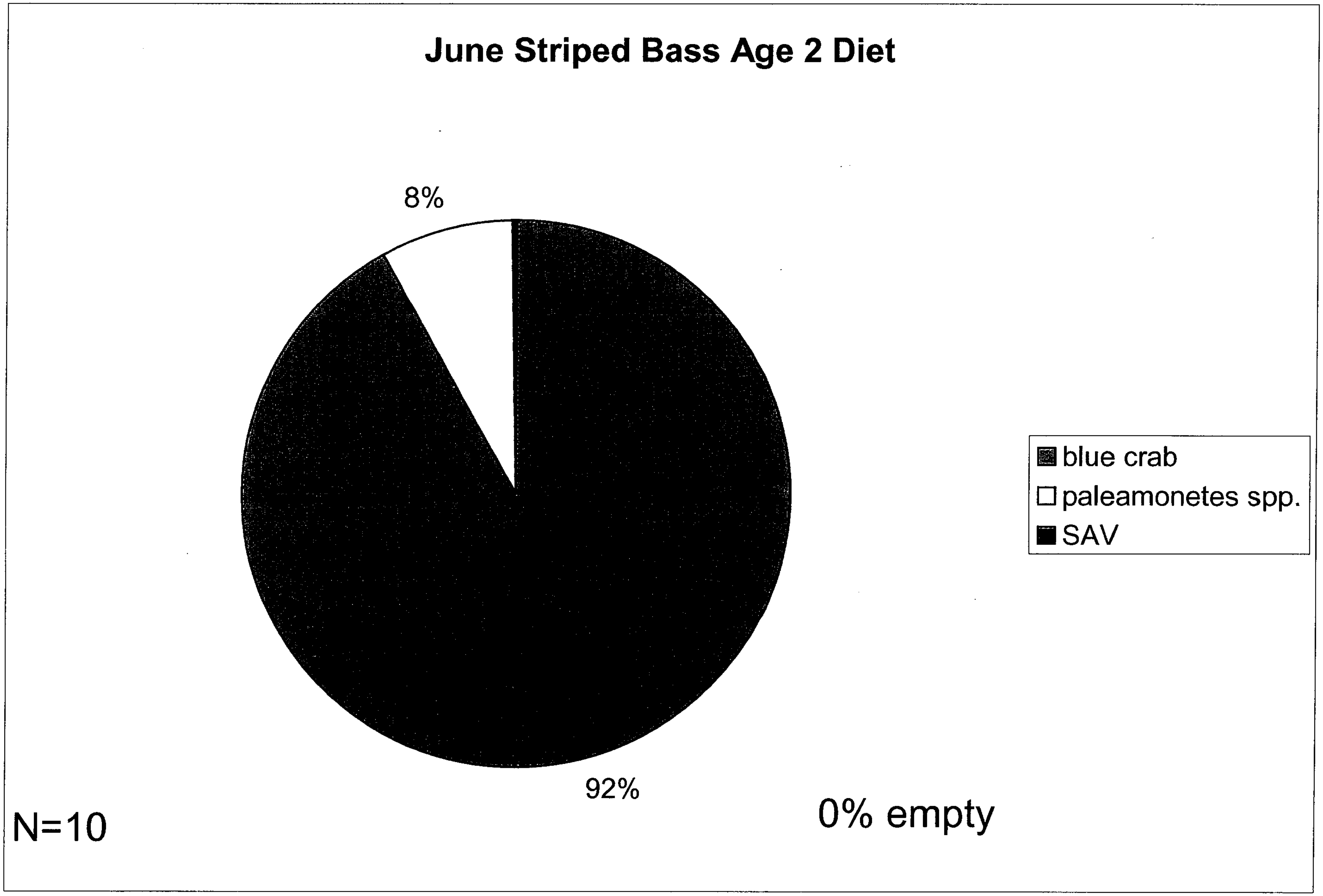
In age 2 fish, blue crab (57%) mass increased and that of smaller crustaceans was greatly reduced. Fish became more important in age 2 increasing cumulative contribution from 21% (age 1) to 30%. Spot (14%), silver perch (12%) and mummichog (3%) were the most notable finfish prey. Interestingly, polychaetes contributed more to age 2 fish (13%) annually than they did to age 1 (<1%). Diet of age 2 fish was less diverse than that of age 1 (Fig. 3.9) and invertebrates continued to be important and dominated diet every month except July. Ninety-seven percent of age 2 fish examined contained only benthic prey. No fish ever contained a mixture of benthic and pelagic prey. Polychaete spp. (13%) content was unusually high in May. Blue crab (10%) and paleamonetes shrimp (<1%) were less important (Fig. 3.10). In June, polychaetes were absent and blue crab (92%) and paleamonetes (8%) dominated diet (Fig. 3.11). Finfish species (combined 90%), in particular silverside spp. (81%), were markedly more important in July than any other month. This seasonal increase in silverside consumption was also evident in age 1 fish (Fig. 3.12). Age 2 fish were not sampled in August or September either. As with age 1 striped

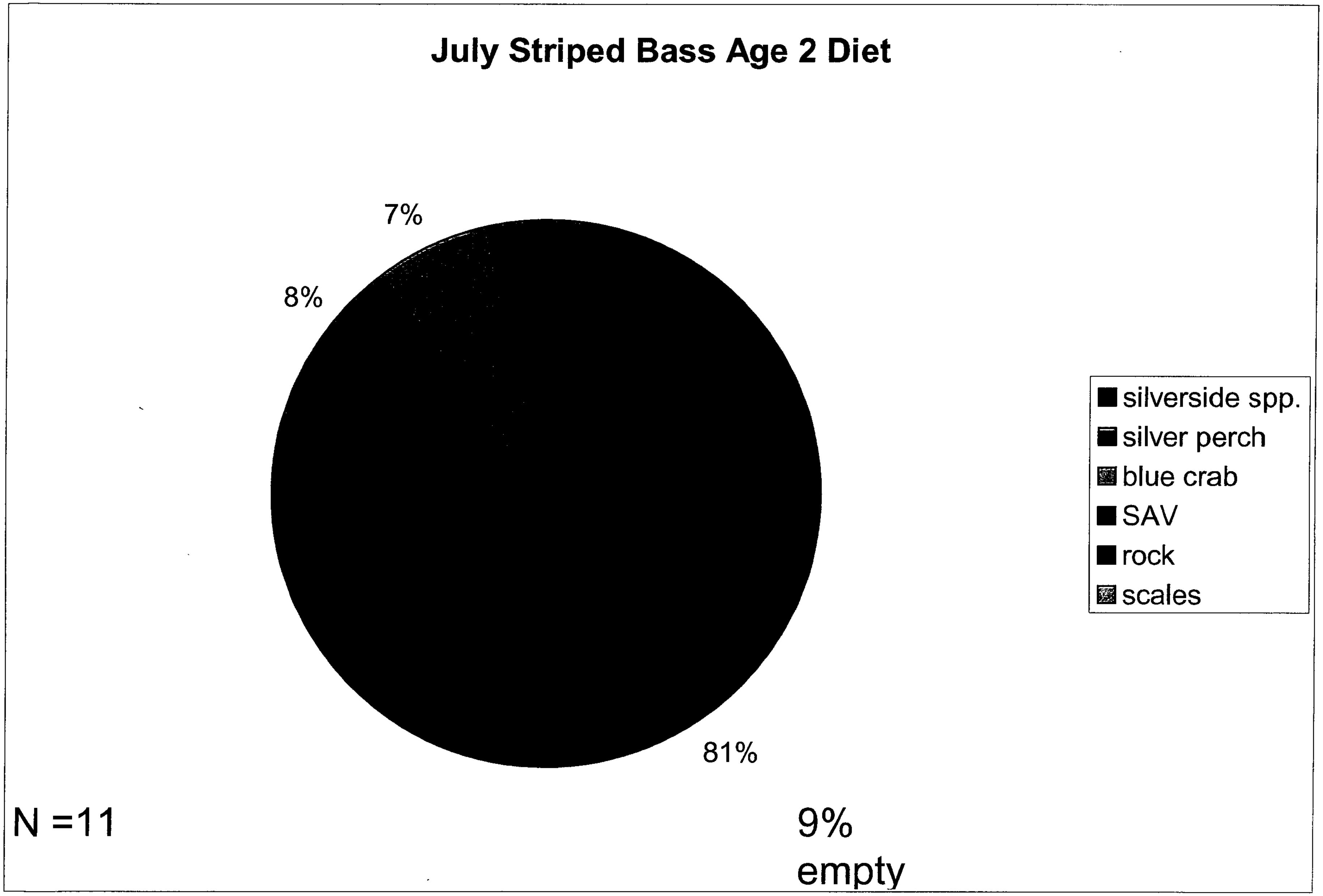
Figures 3.9-3.14. These figures contain pie charts of age 2 fish. Annual content is presented first followed by monthly analysis in order sampled.

Striped Bass Age 2 Annual

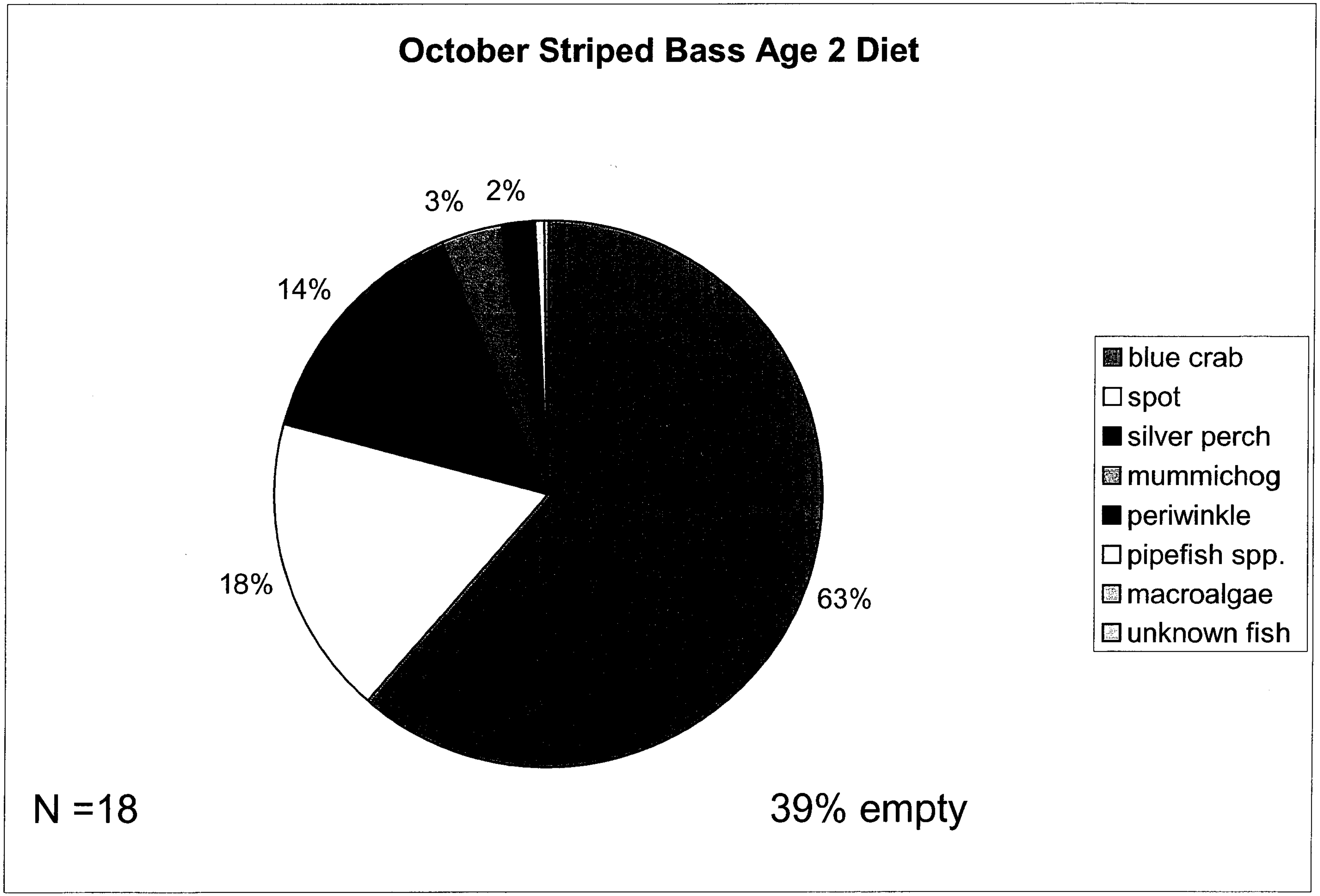


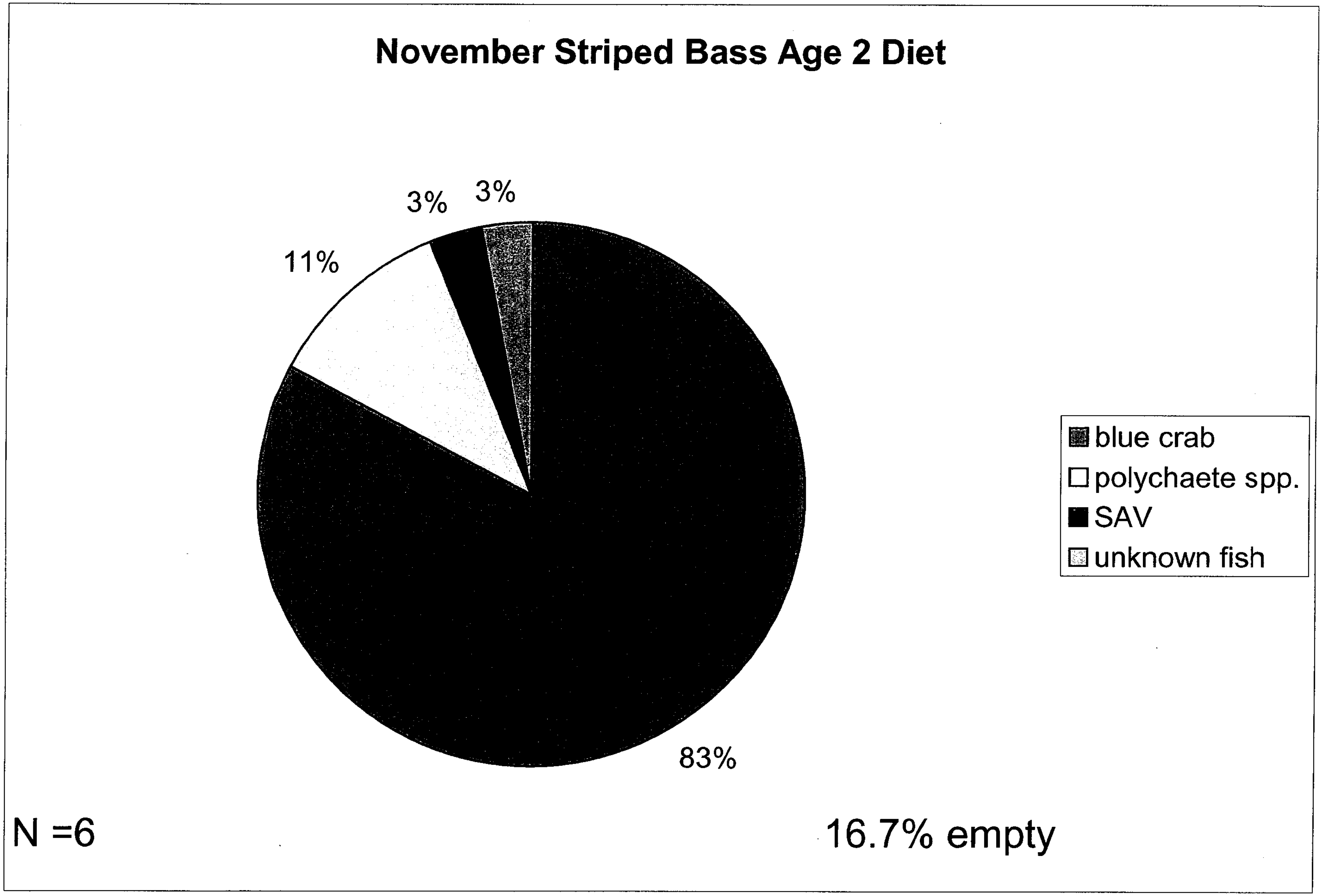

May Striped Bass Age 2 Diet
10%
90%
☐ polychaete spp.
▨ blue crab
☐ paleamonetes spp.
■ SAV
0% empty
N=7


June Striped Bass Age 2 Diet
8%
92%
▨ blue crab
☐ paleamonetes spp.
■ SAV
N=10
0% empty



July Striped Bass Age 2 Diet

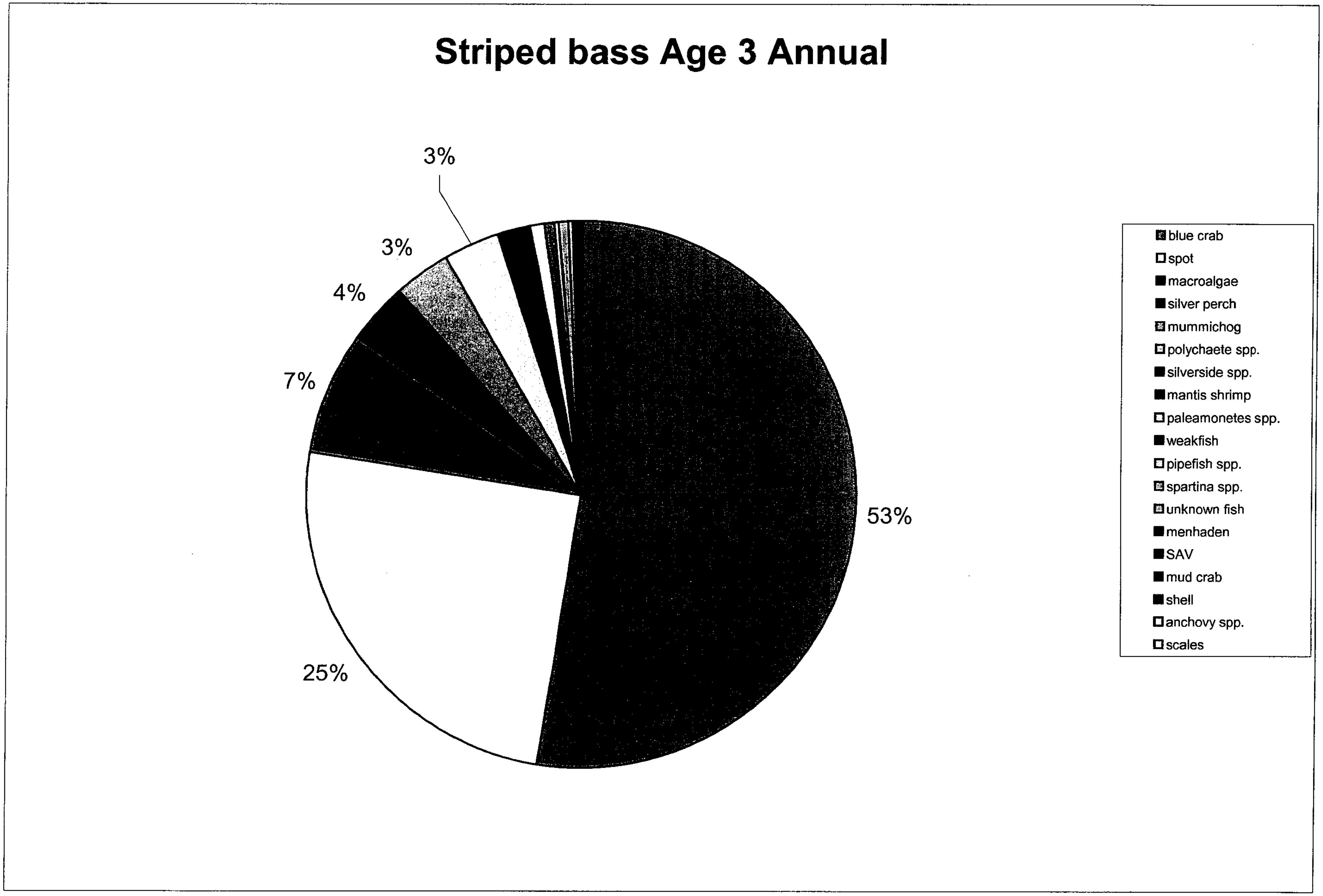

October Striped Bass Age 2 Diet
3%
2%
14%
18%
63%
▨ blue crab
☐ spot
■ silver perch
▨ mummichog
■ periwinkle
☐ pipefish spp.
▨ macroalgae
▨ unknown fish
N =18
39% empty


November Striped Bass Age 2 Diet
3%
3%
11%
83%
▨ blue crab
☐ polychaete spp.
■ SAV
▨ unknown fish
N =6
16.7% empty

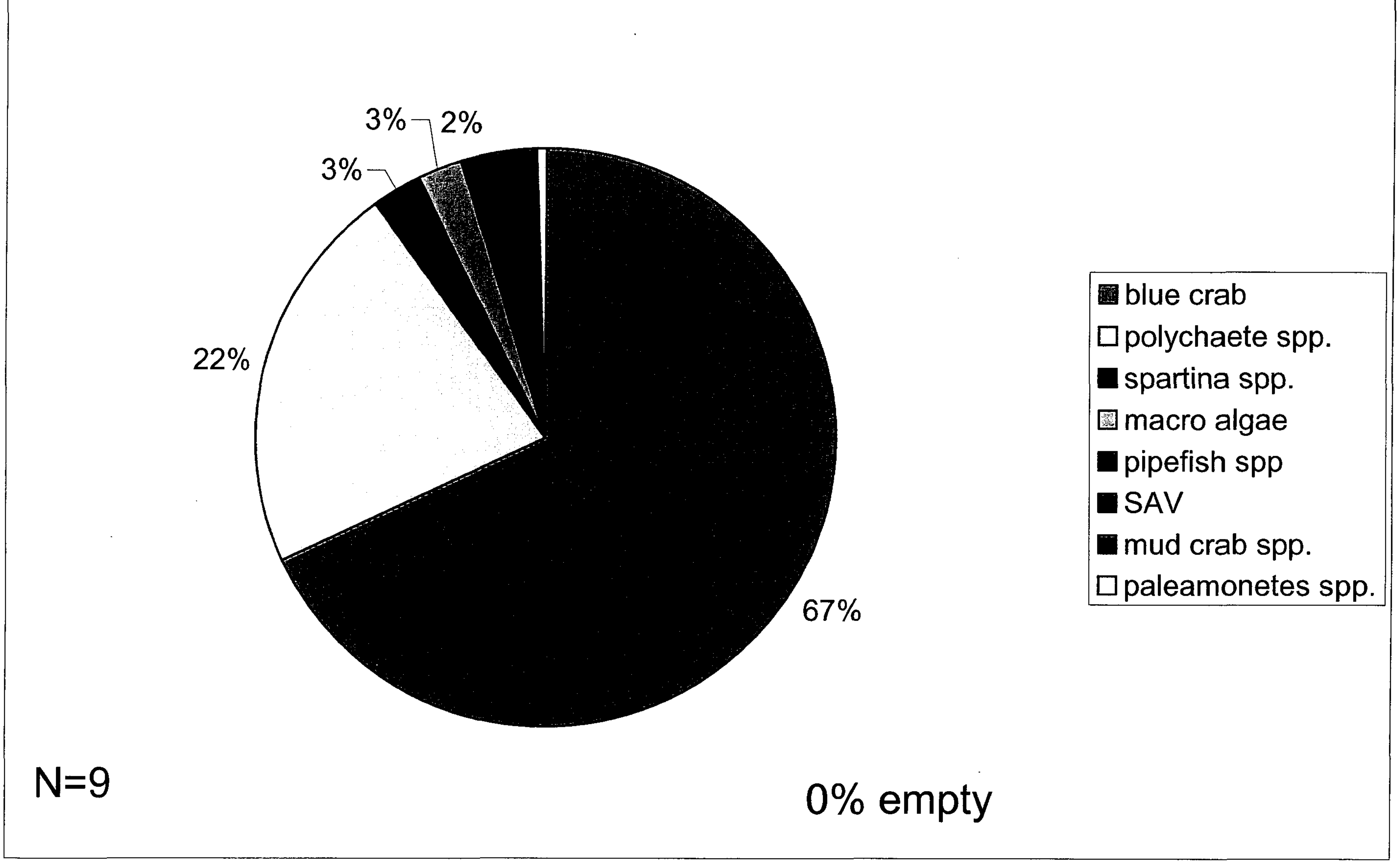
bass age 2 fish returned in October. In age 2 fish, dietary diversity peaked in October (n=8), as did the percentage of empty stomachs (39%). Diet mass was dominated by blue crabs (63%) followed by spot (18%), silver perch (14%) and mummichog (3%) (Fig.3.13). November diet consisted primarily of blue crabs (83%) followed by polychaete spp. (11%)(Fig. 3.14). Dietary diversity (n=4) and percent empty (17%) were reduced along with total age specific catch (n=91 vs. 28).

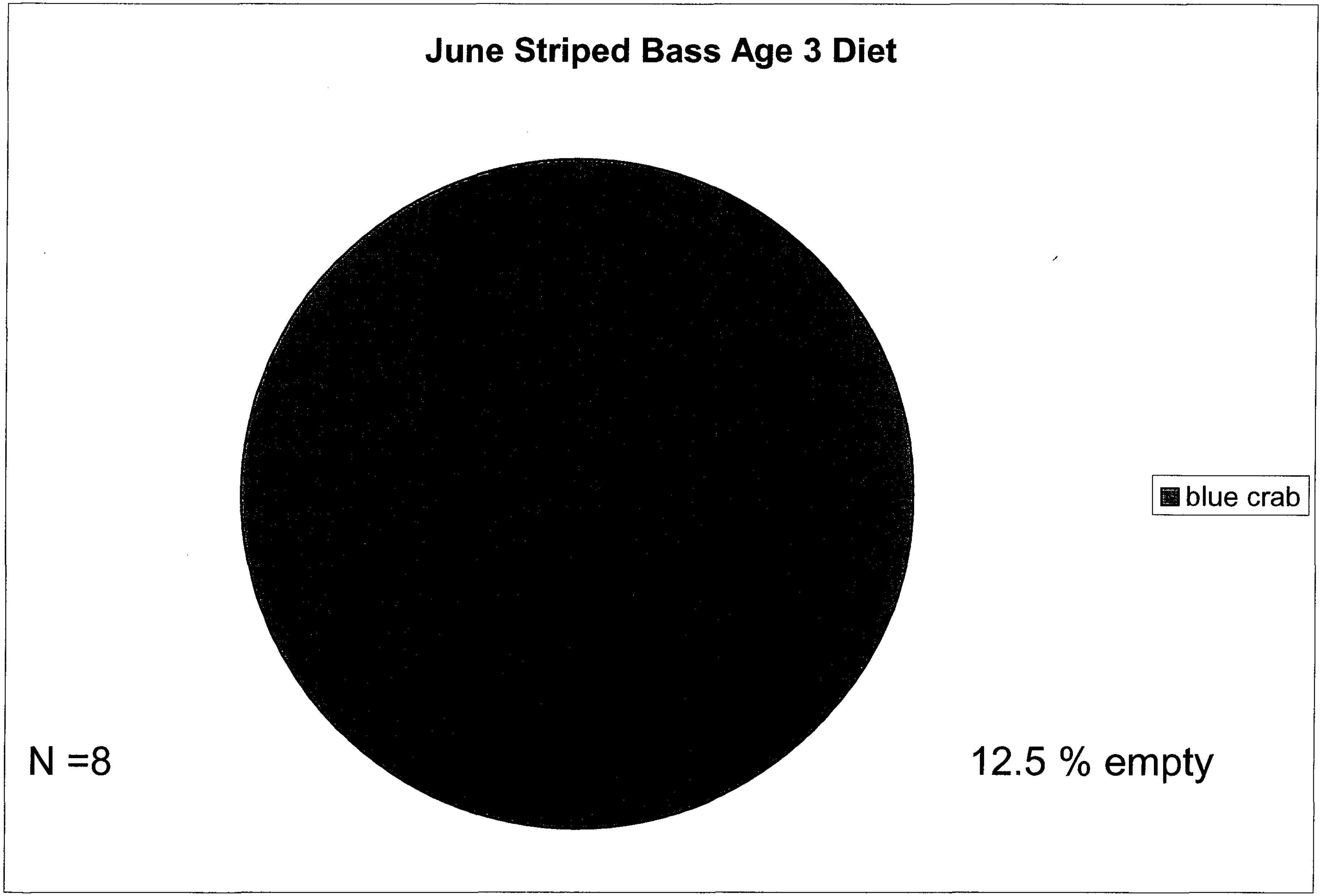
Blue crab (53%) continued to dominate the annual diet of age 3 fish. The same finfish prey species also continued to be important to age 3 striped bass: spot (26%), silver perch (4%), and mummichog (3%). Combined percentage of fish increased from 30% (age 2) to 35% (age 3). Relative shrimp (<1%) biomass was greatly reduced (Fig. 3.15). Most age 3 fish consumed only benthic prey (91%), when pelagic prey was consumed along with benthic (7%) the most often co-occurring species were blue crab and anchovy or silverside spp until late fall when mantis shrimp and menhaden co-occurred. Blue crab (69%) constituted the largest mass of diet in May, but polychaete spp. (21%) also contributed a significant mass during this month (Fig. 3.16). In June, polychaete spp. disappeared from the diet as they had for age 2 fish and diet consisted of only blue crab (100%)(Fig. 3.17). The highest percentage of empty fish (20%) occurred in July. Diet consisted of mostly blue crabs (92%)(Fig. 3.18). As in age 2 fish, age 3 fish showed their greatest diet breadth in October after they too returned from a period of absence. Diet consisted primarily of blue crabs (48%) followed by spot (32%), silver perch (5%), and mummichog (4%)(Fig. 3.19). Finfish species assemblage and order mimicked that

Figures 3.15-3.20. These figures contain pie charts of age 3 fish. Annual content is presented first followed by monthly analysis in order sampled.

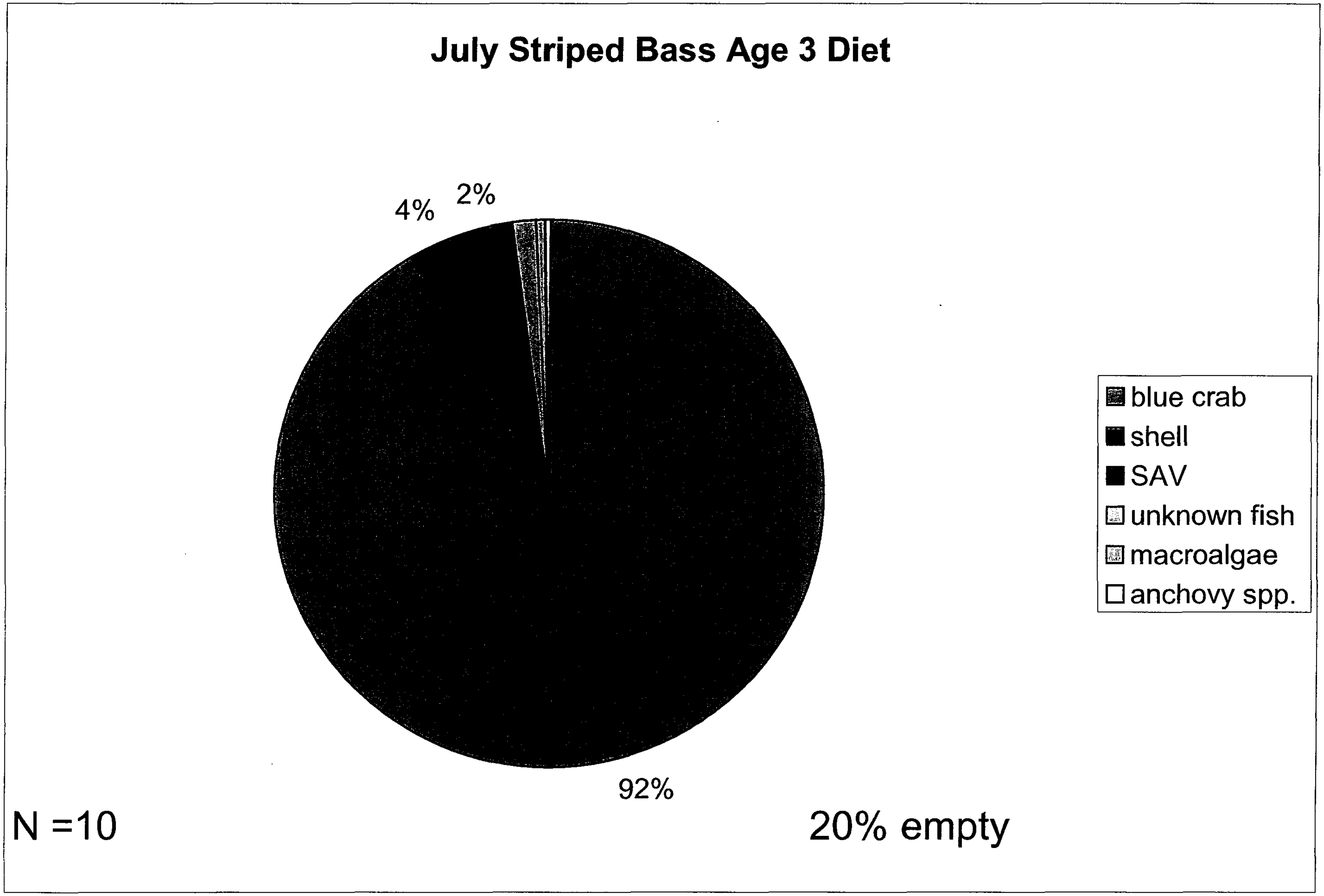

Striped bass Age 3 Annual
3%
3%
4%
7%
53%
25%
blue crab
spot
macroalgae
silver perch
mummichog
polychaete spp.
silverside spp.
mantis shrimp
paleamonetes spp.
weakfish
pipefish spp.
spartina spp.
unknown fish
menhaden
SAV
mud crab
shell
anchovy spp.
scales

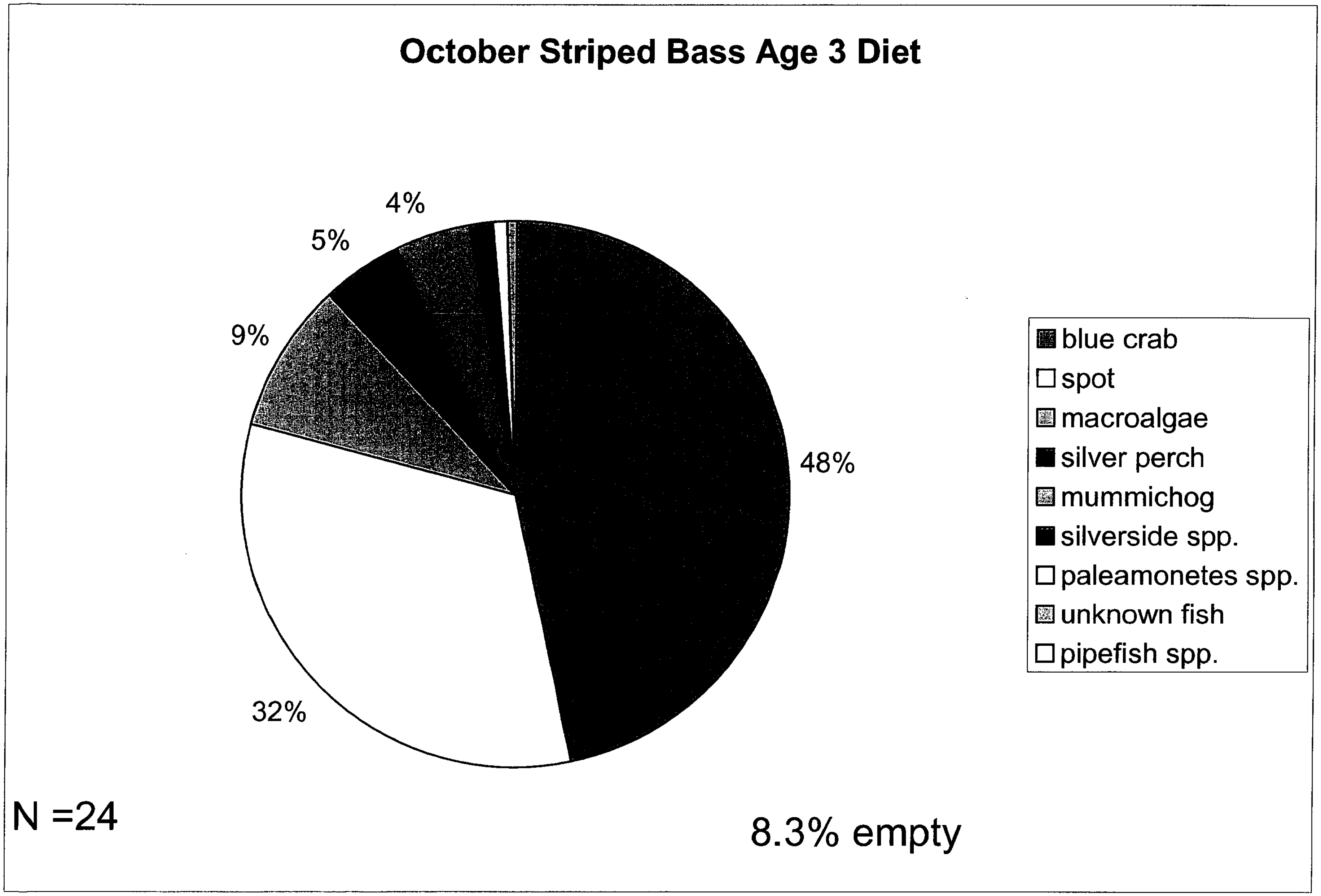
May Striped Bass Age 3 Diet



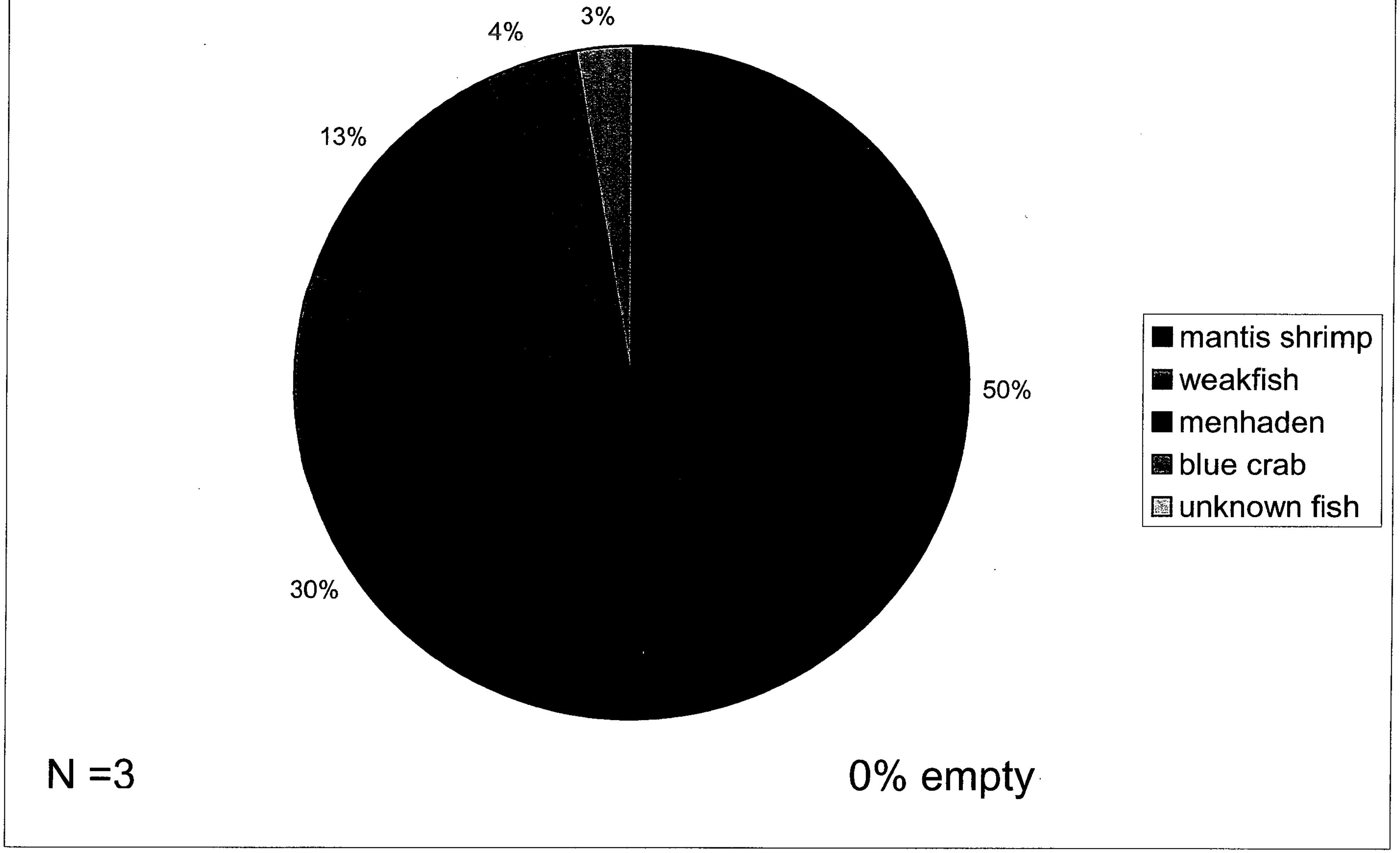


June Striped Bass Age 3 Diet


July Striped Bass Age 3 Diet
4%
2%
92%
N =10
20% empty
▨ blue crab
■ shell
■ SAV
▨ unknown fish
▨ macroalgae
☐ anchovy spp.


October Striped Bass Age 3 Diet
4%
5%
9%
48%
32%
blue crab
spot
macroalgae
silver perch
mummichog
silverside spp.
paleamonetes spp.
unknown fish
pipefish spp.
N =24
8.3% empty

November Striped Bass Age 3 Diet



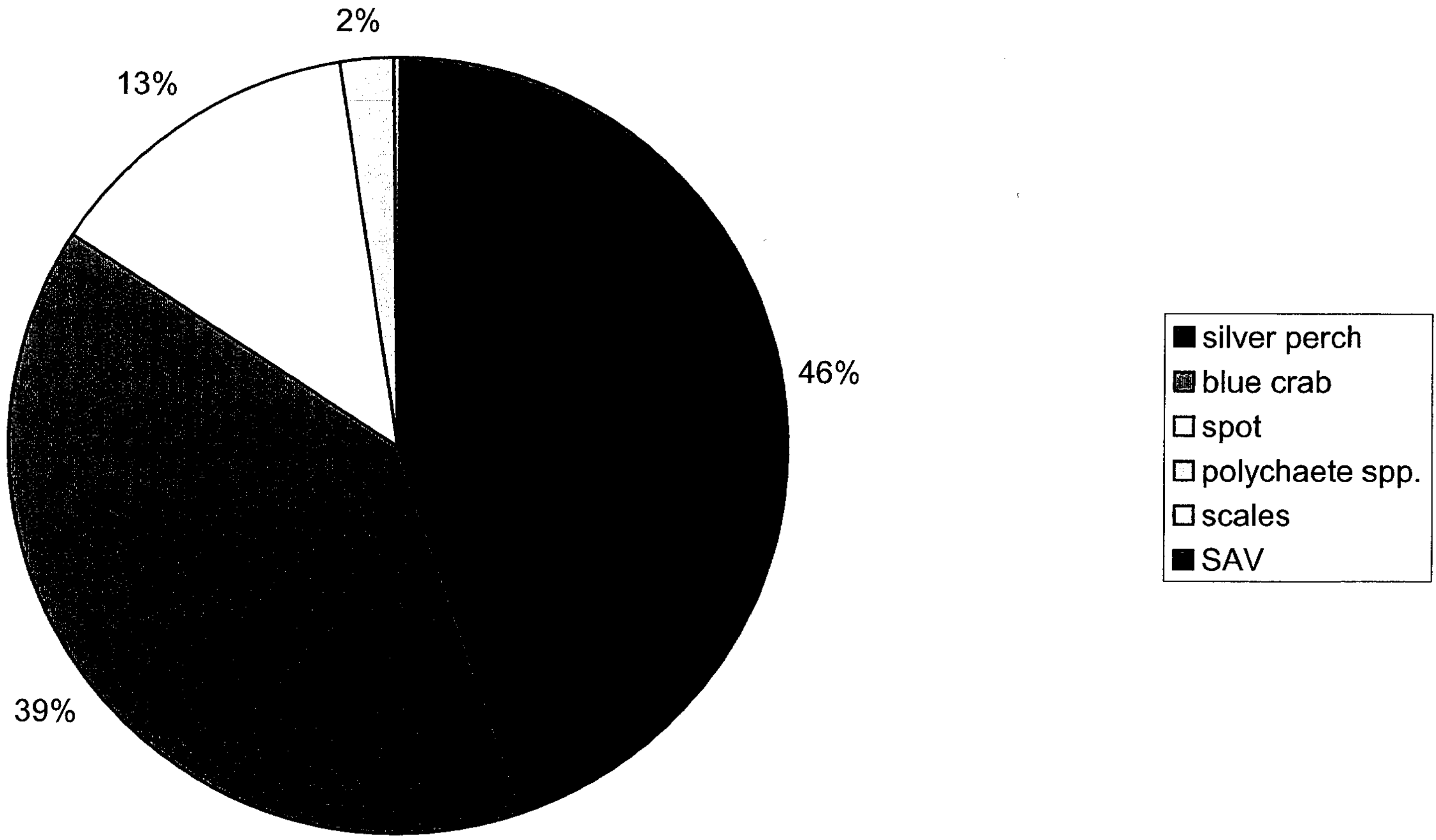
evidenced in age 2 fish during October but cumulative contributions increased by 6%. In November, sample size was reduced (n=3). Mantis shrimp (50%) replaced blue crab (4%) as the dominant crustacean. Weakfish (30%) and menhaden (13%) were also consumed. (Fig. 3.20), but percentage of finfish in diet was reduced from previous month.

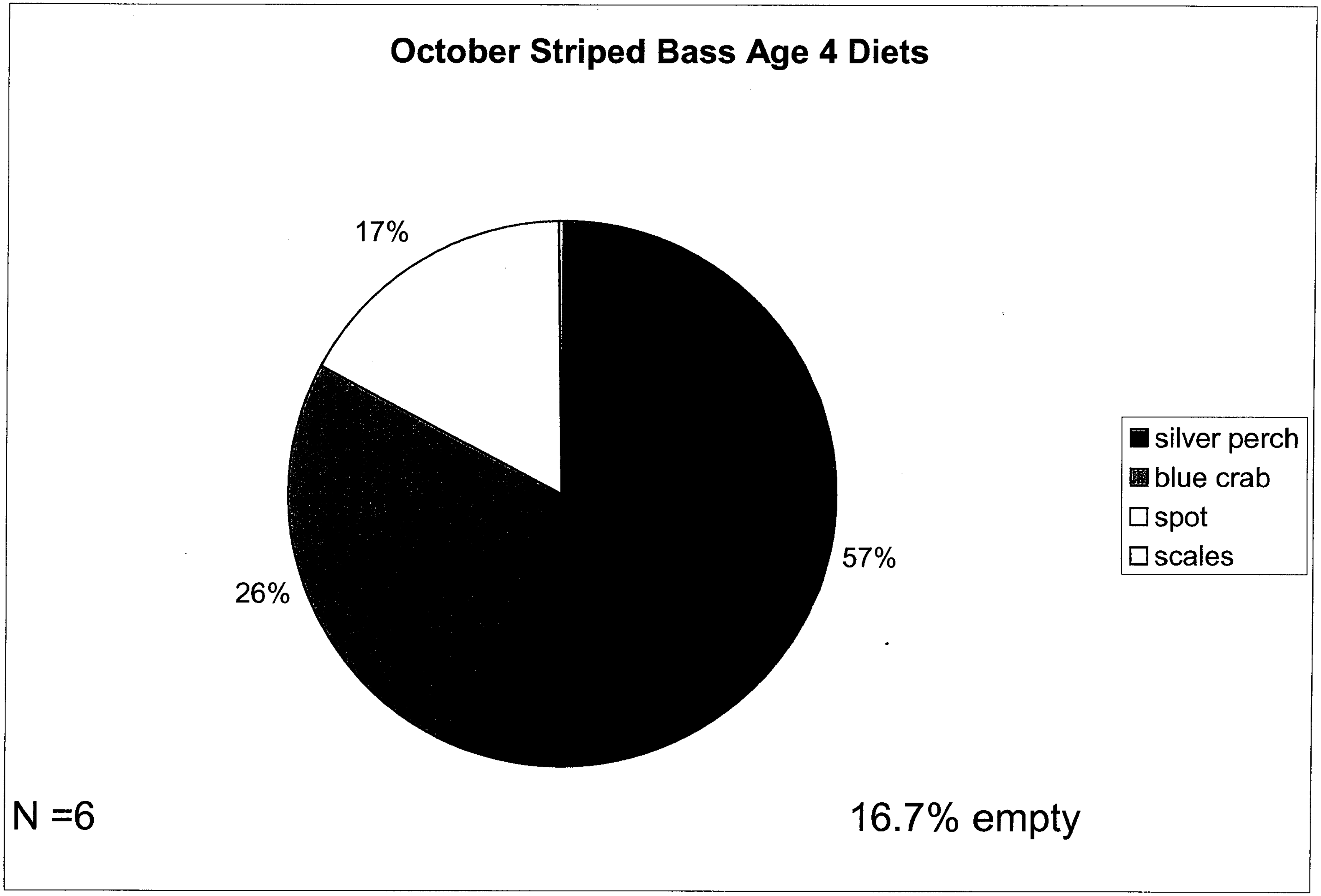
No seasonal comparisons between age 4 fish were possible because significant sample size was only available in October. Small numbers occurred during other months but sample size did not meet minimum of three. Annually, blue crabs (39%) contributed a significant portion of diet (39%) but finfish species in particular silver perch (46%) and spot (13%) were clearly more important than in younger fish (Fig. 3.21). Though age 4 fish relied more heavily on finfish than younger age classes, the species consumed relied solely on benthic resources. Diet was 100% benthic in trophic origin. In October, stomach content was dominated by silver perch (57%) and spot (17%) followed by blue crabs (26%)(Fig. 3.22).

There appears to be a switch in diet in fish above age 4. Total samples size was small (n=12) and biased towards fall (n=9). Annual diet mass was clearly dominated by finfish (67%)(Fig. 3.23). Gizzard shad (48%) silver perch (17%) and mummichog (2%) were all consumed. Blue crab (27%) was still important but large shad consumed dwarfed mass contributions. Sixty percent of diet consisted of benthic prey only. Prey of both benthic and pelagic trophic origin appeared in the gut once in November (mantis shrimp and American eel). Unfortunately, the fall was the

Figures 3.21-3.22. These figures contain pie charts of age 4 fish. Annual content is presented first followed by monthly analysis in order sampled.

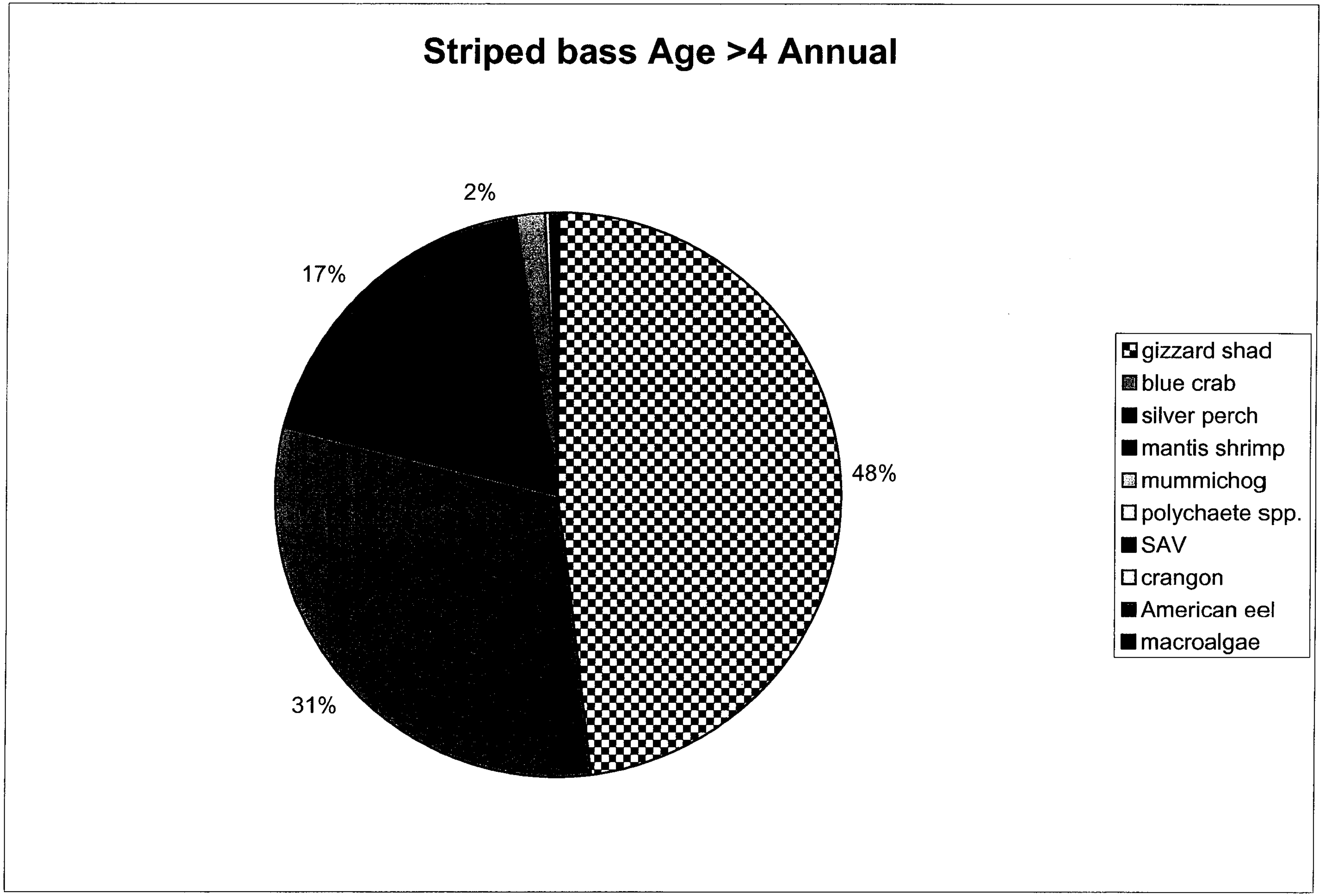
Striped bass Age 4 Annual



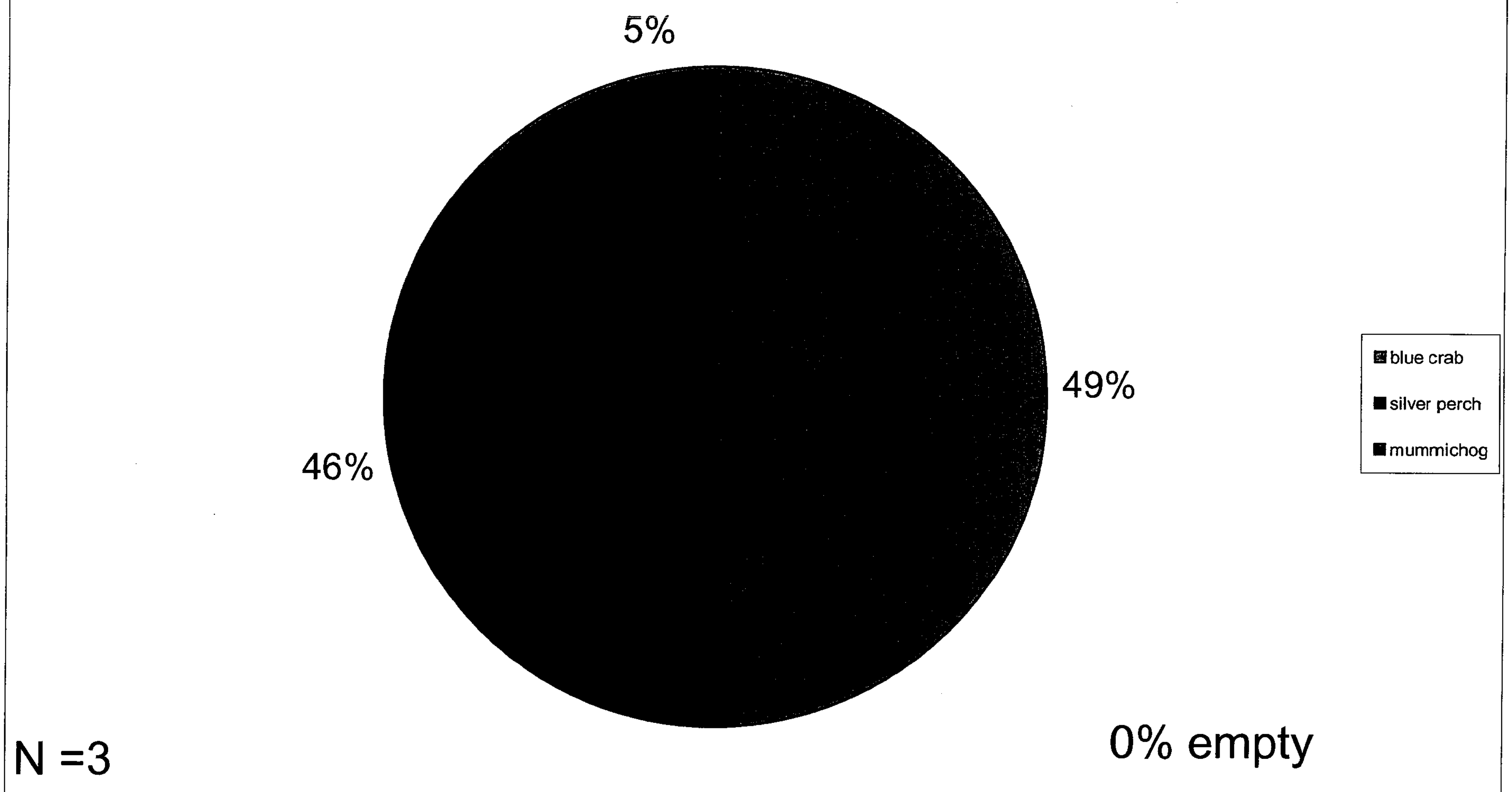


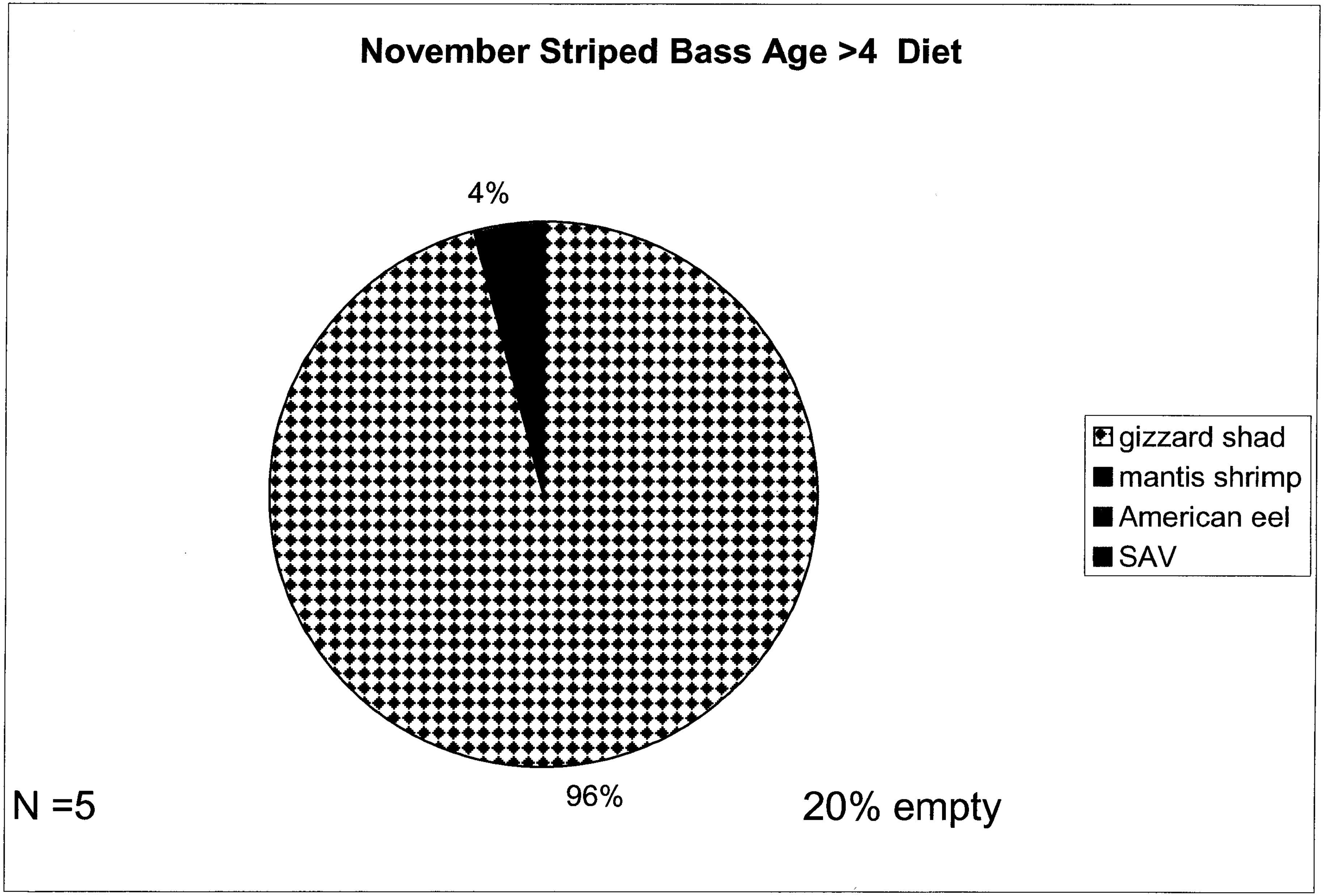
October Striped Bass Age 4 Diets

Figures 3.23-3.25. These figures contain pie charts of age > 4 fish. Annual content is presented first followed by monthly analysis in order sampled.


Striped bass Age >4 Annual
2%
17%
48%
31%
gizzard shad
blue crab
silver perch
mantis shrimp
mummichog
polychaete spp.
SAV
crangon
American eel
macroalgae

October Striped bass Age >4 Diet



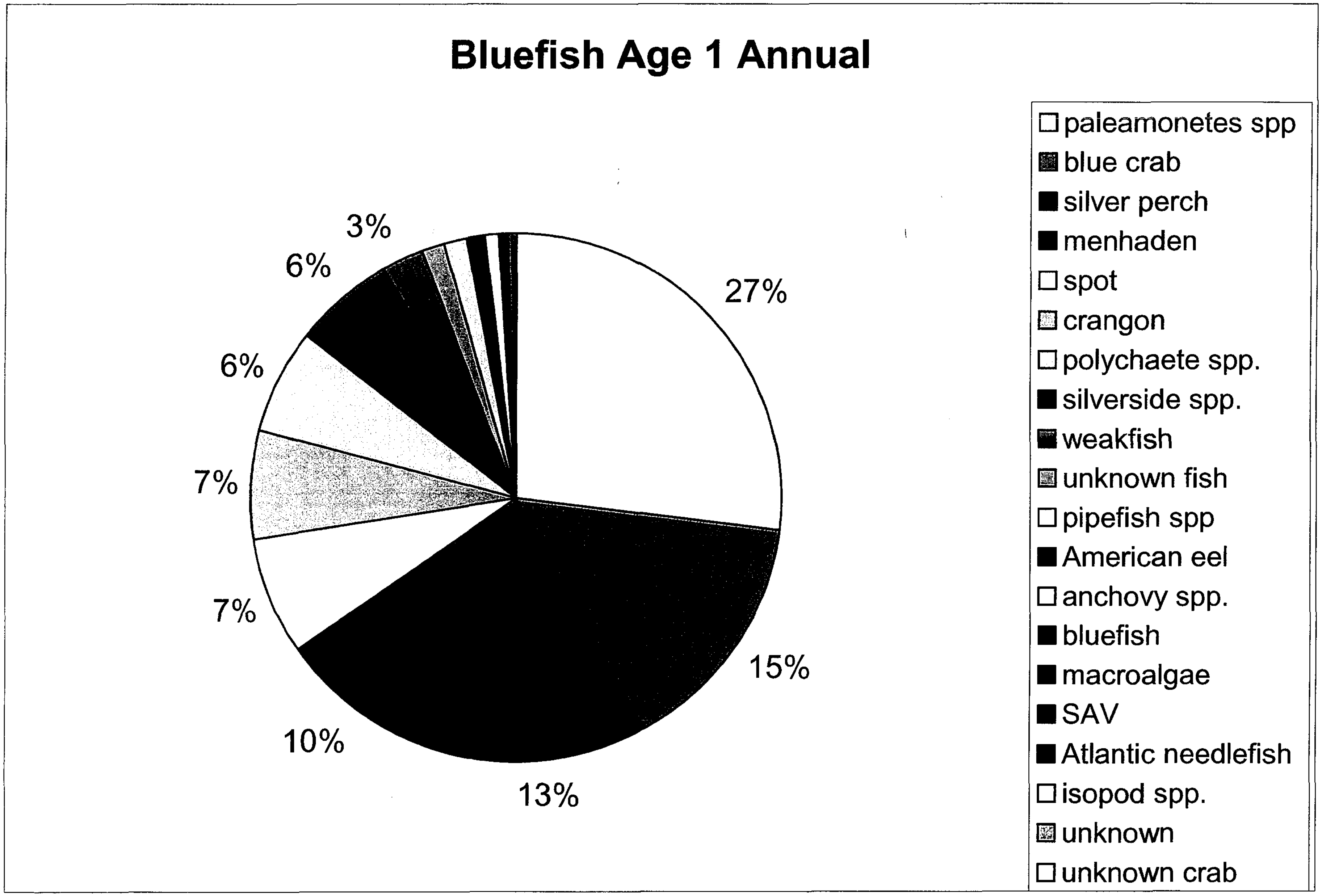

November Striped Bass Age >4 Diet
4%
96%
gizzard shad
mantis shrimp
American eel
SAV
N =5
20% empty

only season when a significant number of these older fish occurred, so seasonal diet comparisons were not possible. Due to this seasonal in abundance it is unclear whether diet alterations in comparison to younger fish are due to ontenogenics or season. What is clear is that the increased mouth gape of these much larger fish allowed them to prey upon the large numbers of gizzard shad in the study site (see Chapter 2 for details) that had previously avoided striped bass predation due to their size. During October, stomach content mass of age 4< fish consisted mostly of blue crab (49%). The smallest fish in the age class occurred during this month and it is likely that they were not yet large enough to target available gizzard shad (Fig. 3.24). Blue crab abundance in the study site was greatly reduced in November when mantis shrimp (4%) appeared to replace blue crab in diet. A similar increase in importance of mantis shrimp occurred in November for age 3 fish. Gizzard shad (n=3) were 96% of the mass consumed during this month (Fig. 3.25).

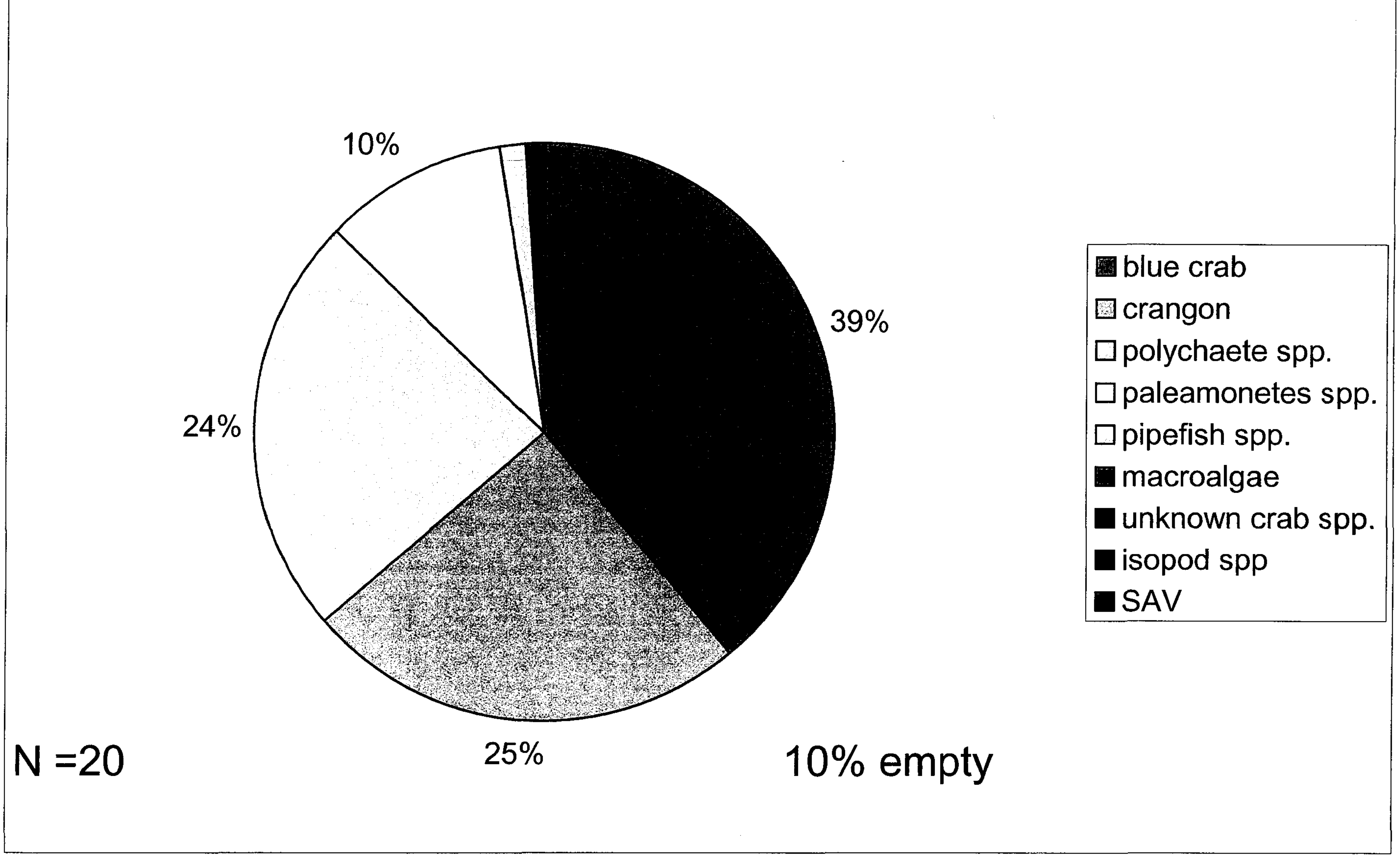
Bluefish

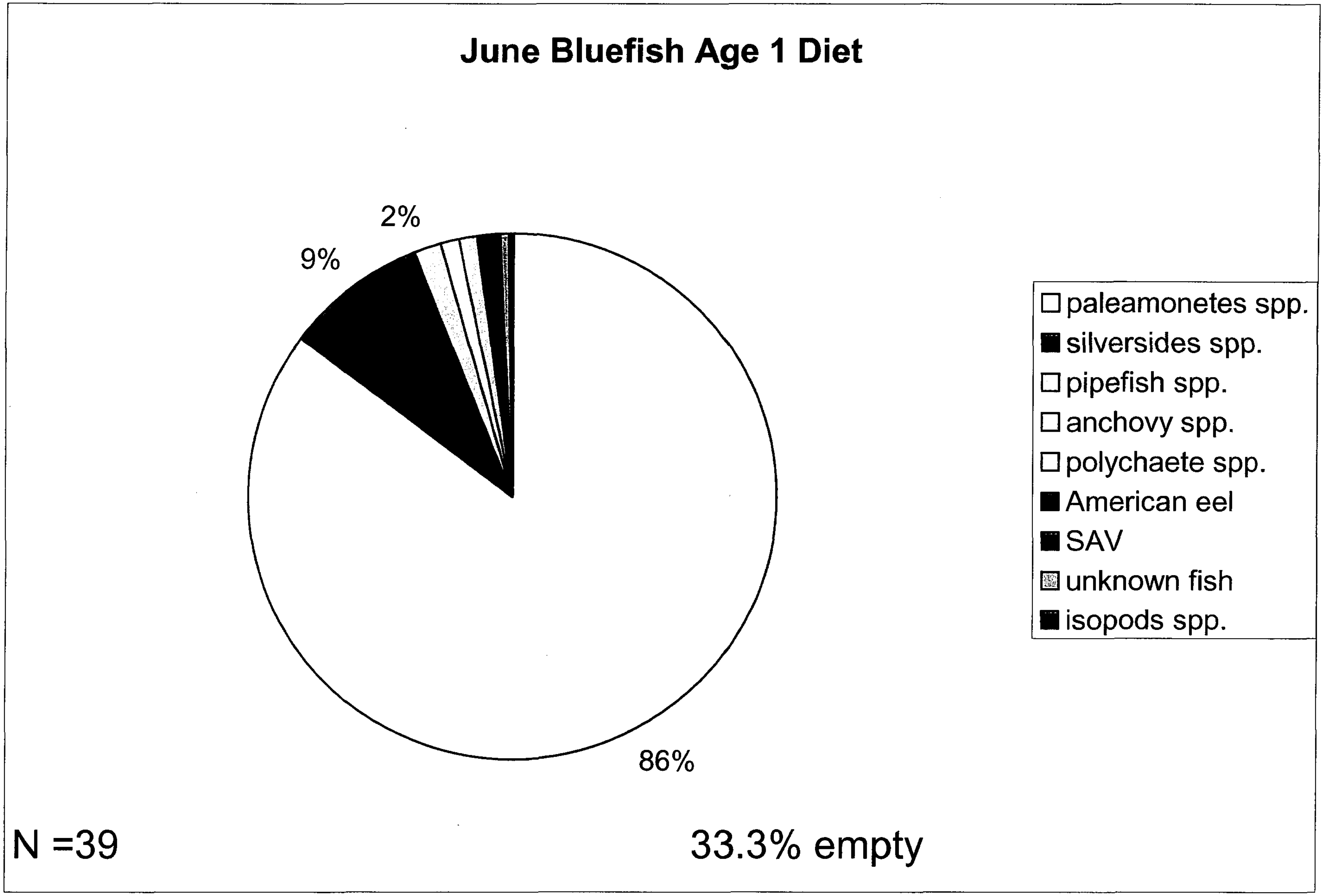
Annually age 1 bluefish diet was diverse consisting of 20 different prey categories. Diet was dominated by crustaceans principally paleamonetes shrimp (27%), blue crab (15%) and crangon (7%). The most important finfish prey were silver perch (13%), menhaden (10%), spot (7%) and silverside spp. (6%)(Fig. 3.26). Sixty percent of stomachs examined contained only benthic prey. Twenty-one percent contained prey that was benthic and pelagic in trophic origin. Silverside spp. and anchovy occurred mixed with paleamonetes in the spring and summer.

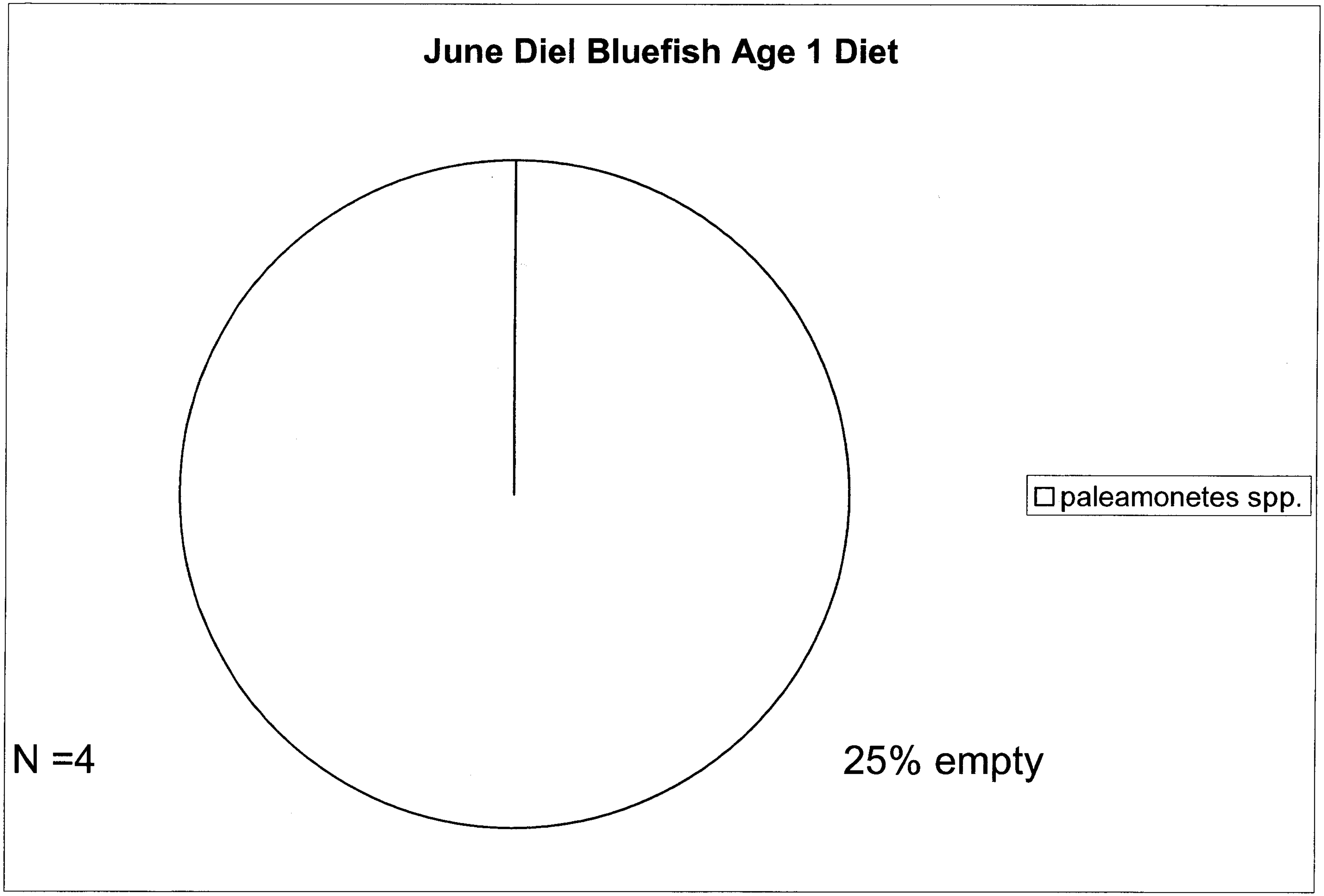
Figures 3.26-3.33. These figures contain pie charts of age 1 bluefish. Annual content is presented first followed by monthly analysis in order sampled.

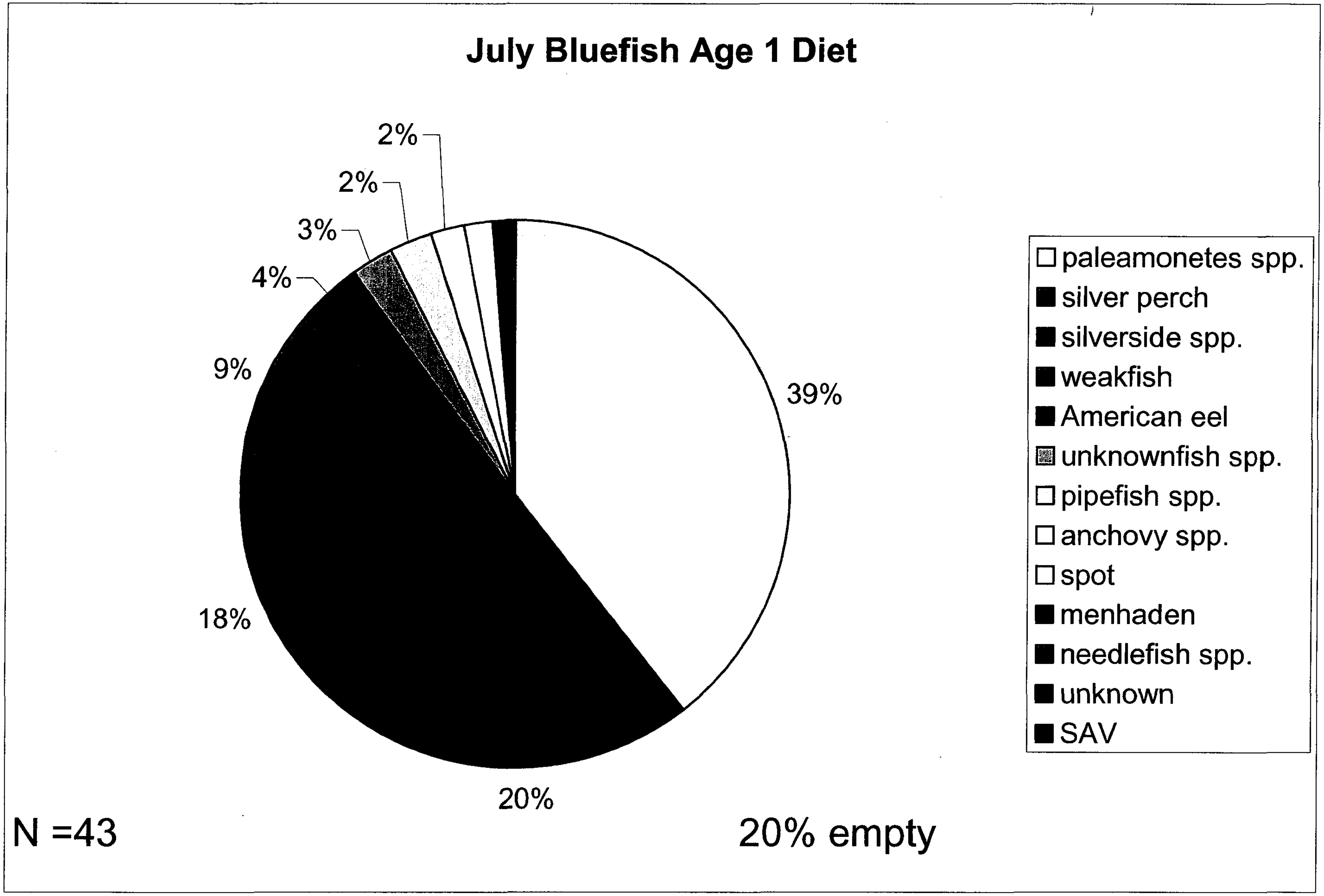

Bluefish Age 1 Annual
27%
15%
13%
10%
7%
7%
6%
6%
3%
☐ paleamonetes spp
▨ blue crab
■ silver perch
■ menhaden
☐ spot
▨ crangon
☐ polychaete spp.
■ silverside spp.
▨ weakfish
▨ unknown fish
☐ pipefish spp
■ American eel
☐ anchovy spp.
■ bluefish
■ macroalgae
■ SAV
■ Atlantic needlefish
☐ isopod spp.
▨ unknown
☐ unknown crab

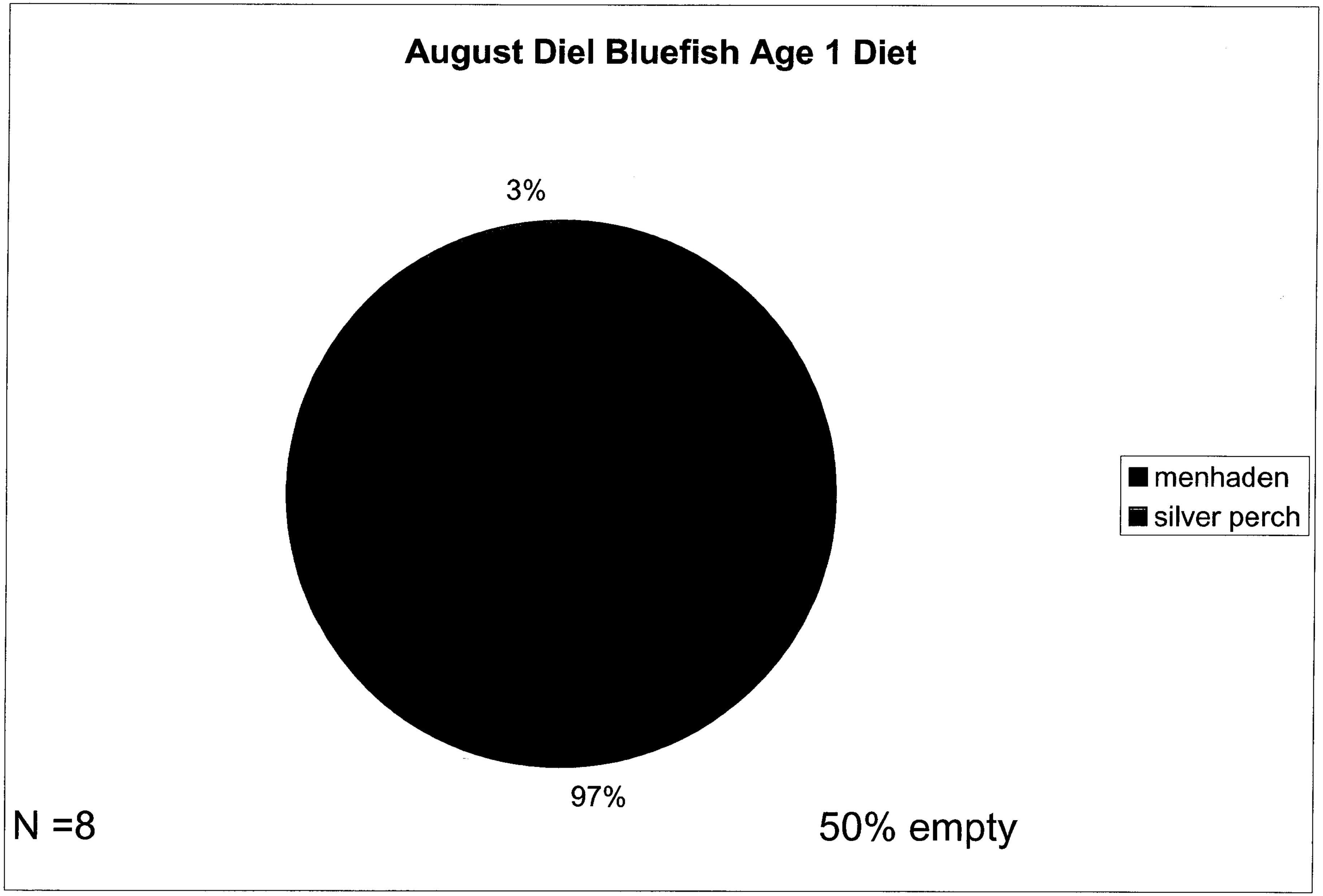
May Bluefish Age 1 Diet

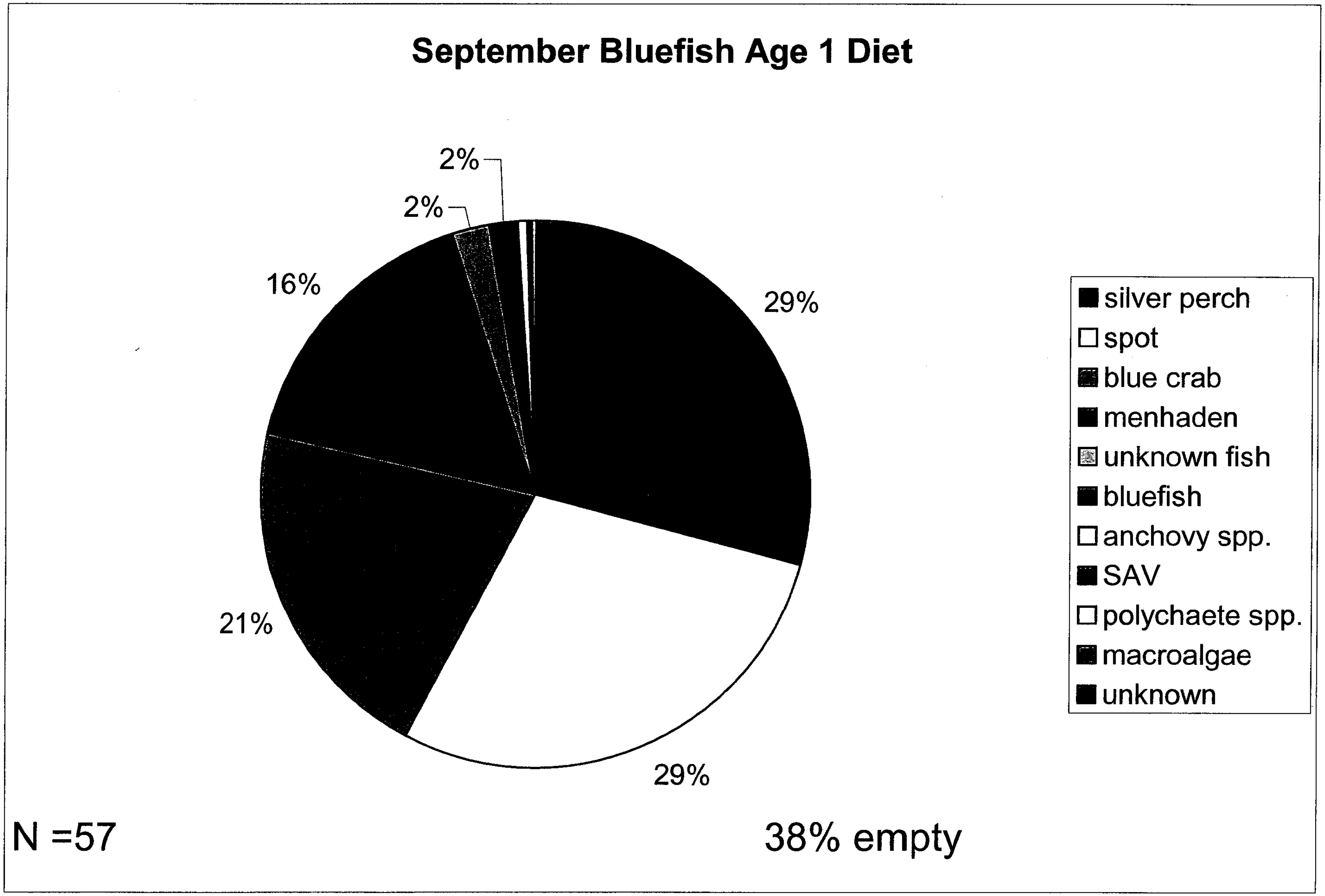


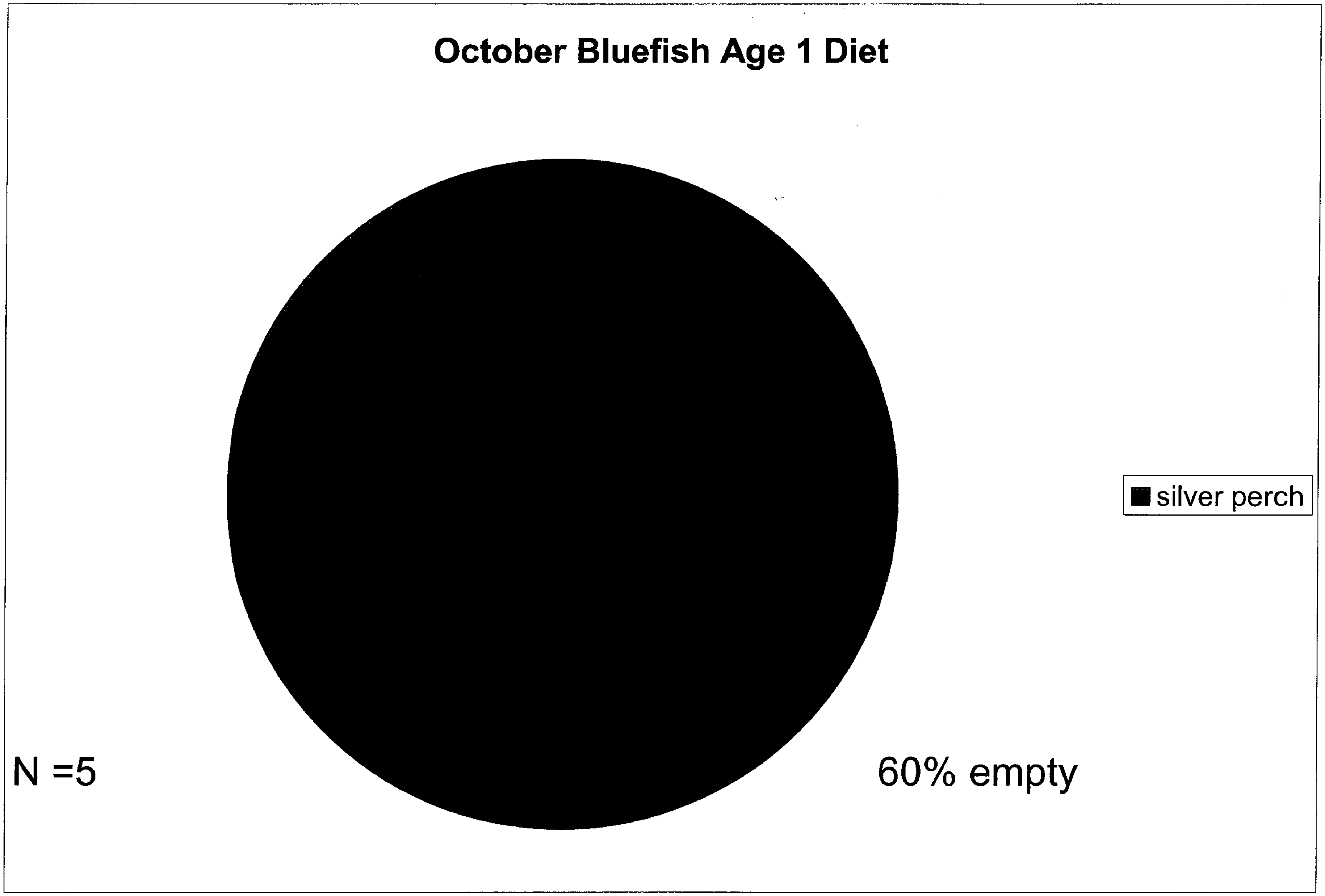

June Bluefish Age 1 Diet
2%
9%
86%
☐ paleamonetes spp.
■ silversides spp.
☐ pipefish spp.
☐ anchovy spp.
☐ polychaete spp.
■ American eel
■ SAV
▨ unknown fish
■ isopods spp.
N =39
33.3% empty


June Diel Bluefish Age 1 Diet
☐ paleamonetes spp.
N =4
25% empty


July Bluefish Age 1 Diet
2%
2%
3%
4%
9%
18%
20%
39%
☐ paleamonetes spp.
■ silver perch
■ silverside spp.
■ weakfish
■ American eel
▨ unknownfish spp.
☐ pipefish spp.
☐ anchovy spp.
☐ spot
■ menhaden
■ needlefish spp.
■ unknown
■ SAV
N =43
20% empty


August Diel Bluefish Age 1 Diet
3%
97%
■ menhaden
■ silver perch
N =8
50% empty


September Bluefish Age 1 Diet
2%
2%
16%
29%
21%
29%
silver perch
spot
blue crab
menhaden
unknown fish
bluefish
anchovy spp.
SAV
polychaete spp.
macroalgae
unknown
N =57
38% empty

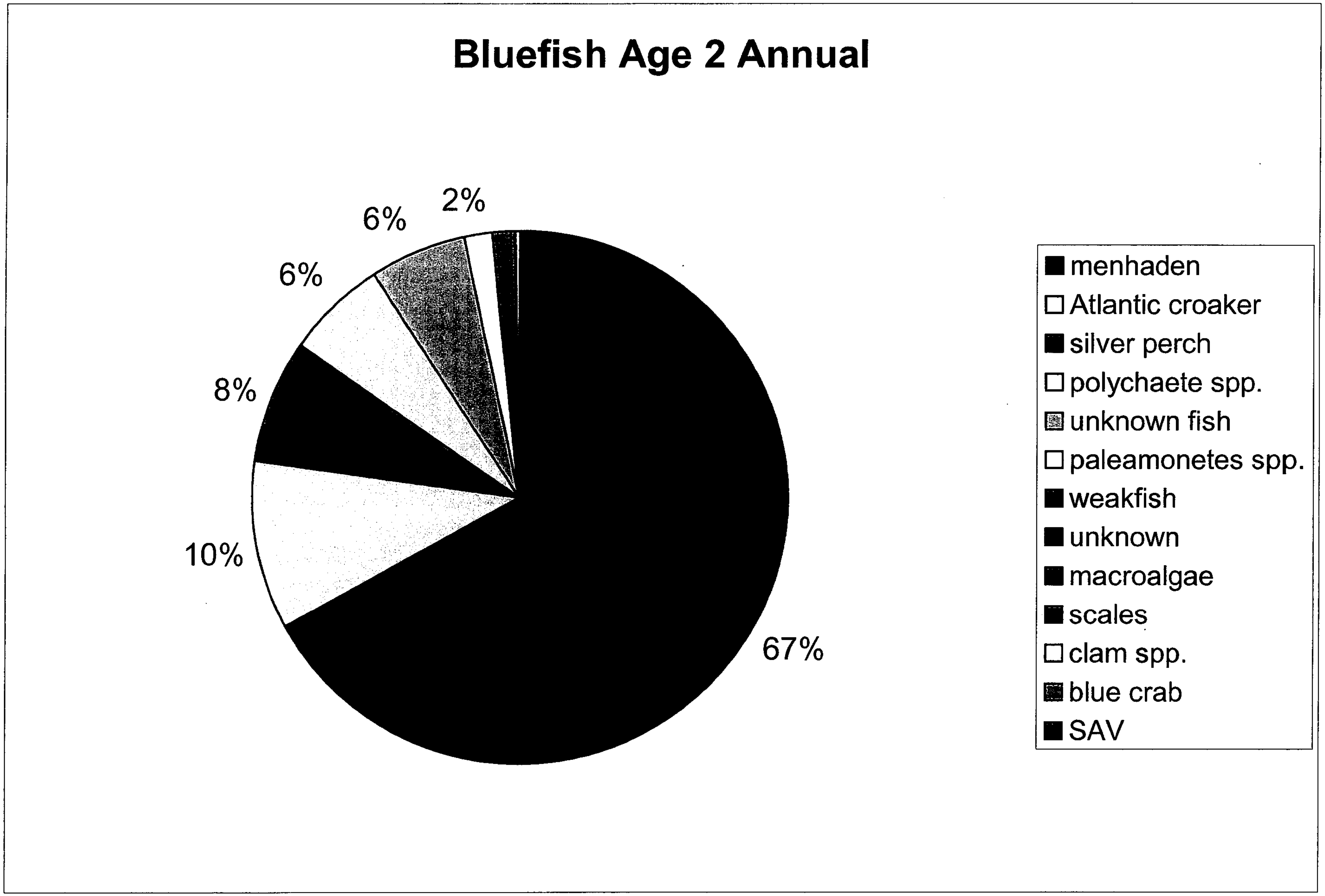


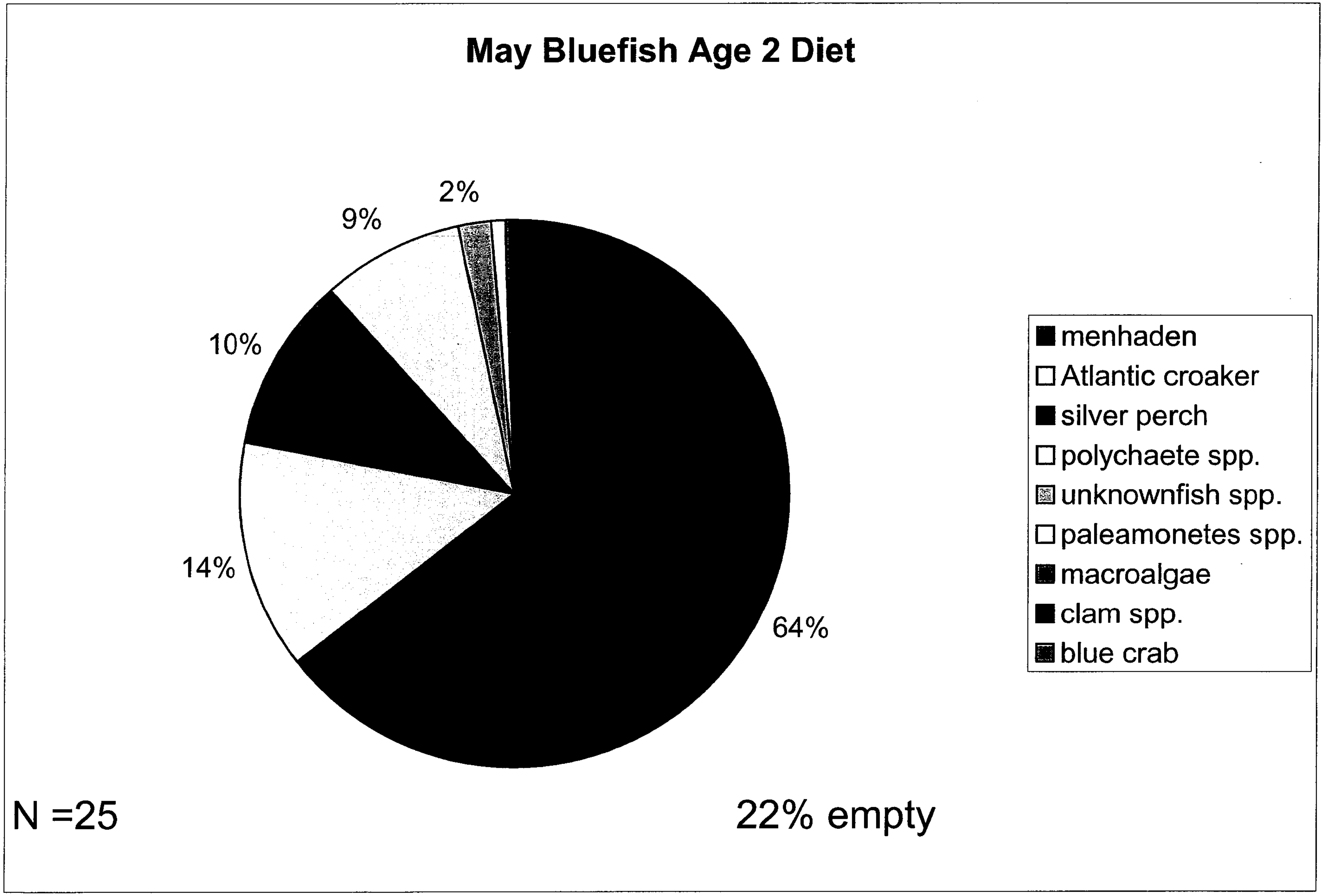
October Bluefish Age 1 Diet

Menhaden became increasingly important in September and remained the dominant pelagic resource until study period ended. Menhaden was found in gut content along side silver perch and blue crab, but 78% of the time that it was found it was found alone. Monthly analysis shows seasonal trends, including an increased importance of finfish as study season progressed. May diet was dominated by blue crab (39%) and crangon shrimp (25%) (Fig. 3.27). As in striped bass May diets, a large mass percentage and high IRI% (Appendix 14) mark the importance of polychaetes to both species during this month. In the June nocturnal sample, paleamonetes spp. (86%) were far more important to age 1 bluefish than finfish species (silverside spp., pipefish spp., anchovy spp., combined 12%, Fig. 3.28). A diel sample on June 19 contained bluefish that had fed solely on paleamonetes shrimp (Fig. 3.29). Low sample size (n=4), however, likely underestimates actual prey diversity. Nocturnal July samples were much more robust with respect to fish number (n=43) and stomach content diversity (n=13 categories). Paleamonetes spp. (39%) continued to dominate diet mass in July but finfish diversity and mass were augmented. In May, finfish contributions were negligible; importance grew to 12% in June. Combined in July nine finfish species contributed approximately 57%. Silver perch (20%), silverside spp. (18%) and weakfish (9%) were most important (Fig. 3.30). Interestingly, age 1 bluefish increased dependence on silverside spp. in July mimics that evidenced in age 1 and 2 striped bass monthly analysis. Stomachs attained from a diel sample in August contained only finfish mostly menhaden (97%). Silver perch made up the rest of the content (3.31). Menhaden continued to be important in September diet (nocturnal) followed by silver perch (29%) and spot (29%) (Fig. 3.32). A considerable mass of blue crab (21%) was also found. Bluefish abundance declined drastically in the fall, October was the last month in which enough age 1 bluefish were sampled. Diet consisted solely of silver perch and 60% of fish examined (n=5) were empty (Fig. 3.33).

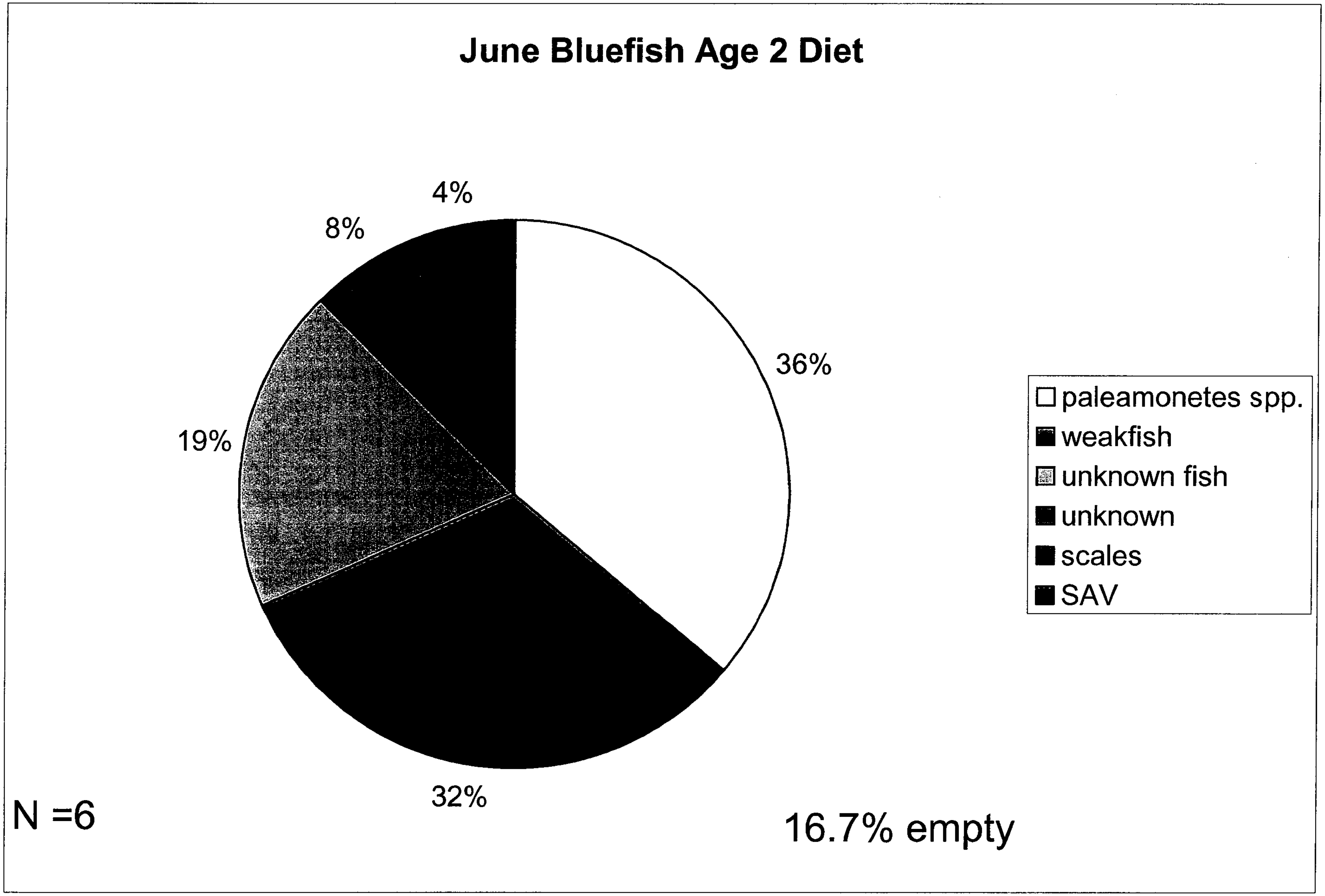
No age 2 fish were sampled after June in the study site. Diet content is, therefore, based on analysis of fish that predominantly occurred during May. Sixty-eight percent of the stomachs examined contained benthic prey alone and the remainder contained pelagic prey. Benthic and pelagic species were not found together. Age 2 bluefish contained a smaller number of prey items than age 1's and diet mass was clearly pelagically dominated (i.e. menhaden was much more important, Fig. 3.34). Menhaden was 67% of the diet by mass followed by Atlantic croaker (10%) and silver perch (8%). Invertebrates (i.e. polychaetes, paleamonetes spp. and clam spp.) were consumed but relative contributions were greatly reduced with respect to age 1 fish. Polychaete spp., contributed a surprisingly large mass annually. This mass was likely due to the large sample size (n=44) in May, which contained an unusually high mass of polychaete species. Though May diet was dominated by a few large menhaden (64%) polychaetes spp. made up 9% of the total mass and many of these smaller prey were regurgitated on capture. Atlantic croaker (14%) and silver perch (10%) made up the bulk of the remaining mass (Fig. 3.35). June was the last month that a significant number of age 2 fish stomachs were examined (n=6). Before age 2 fish left the study site June diet switched to one dominated by paleamonetes spp. (36%). This diet more closely resembled age 1 fish

Figures 3.34-3.36. These figures contain pie charts of age 2 bluefish. Annual content is presented first followed by monthly analysis in order sampled.


Bluefish Age 2 Annual
67%
10%
8%
6%
6%
2%
■ menhaden
☐ Atlantic croaker
■ silver perch
☐ polychaete spp.
▨ unknown fish
☐ paleamonetes spp.
■ weakfish
■ unknown
■ macroalgae
■ scales
☐ clam spp.
▨ blue crab
■ SAV



May Bluefish Age 2 Diet



June Bluefish Age 2 Diet

N =6

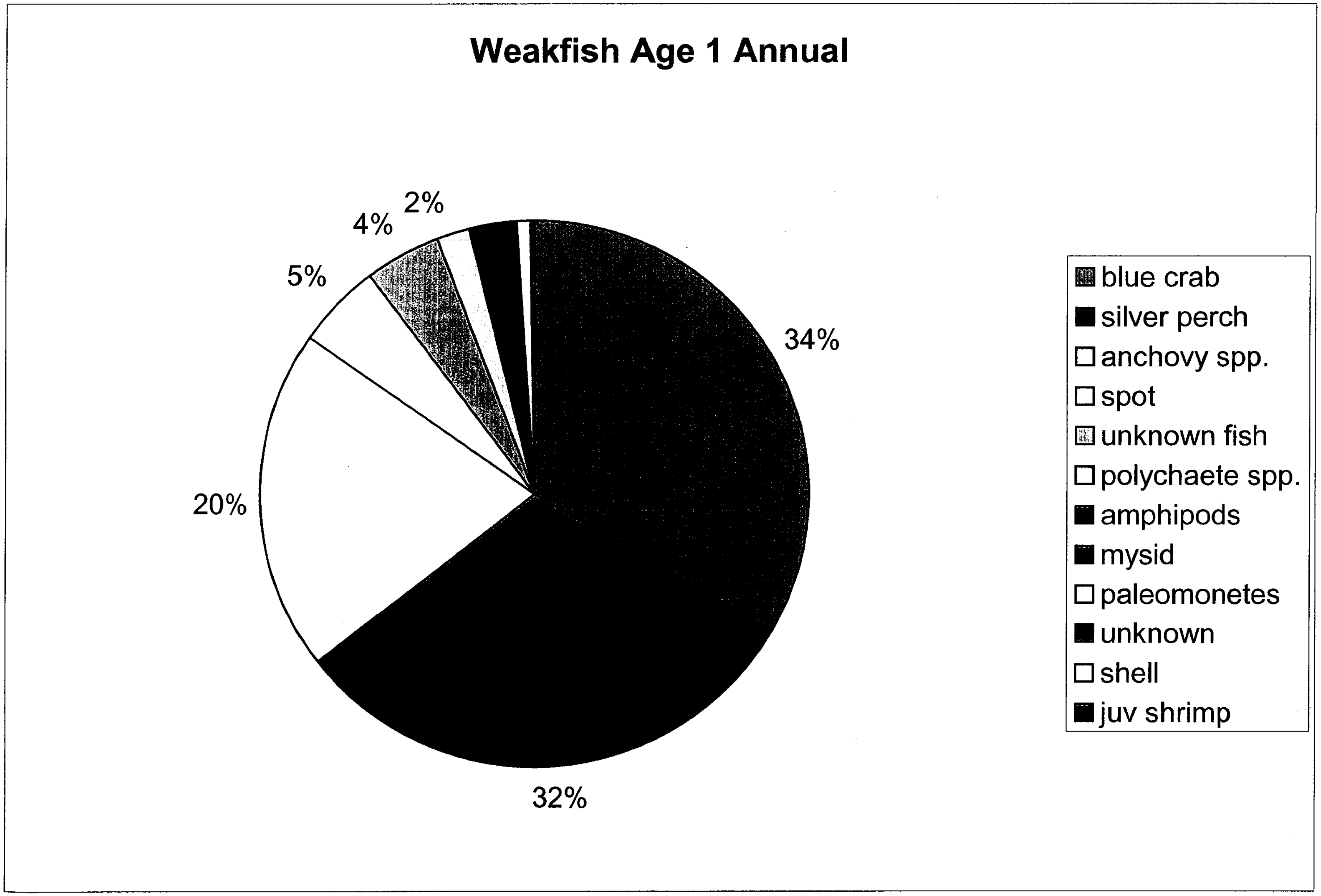
16.7% empty

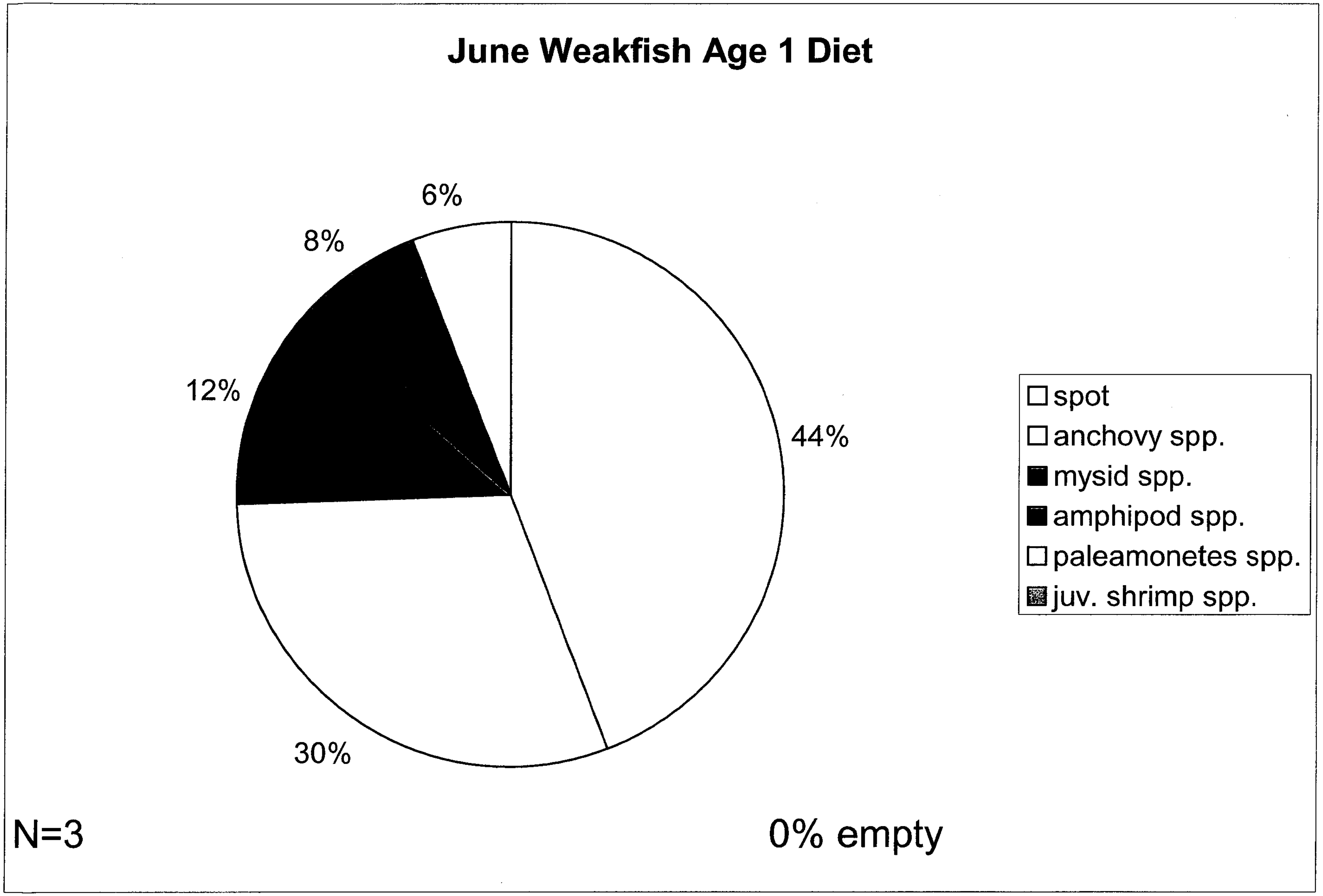
during the period. A small number of weakfish, which contributed a significant mass (32%), were also prey upon (Fig. 3.36).

Weakfish

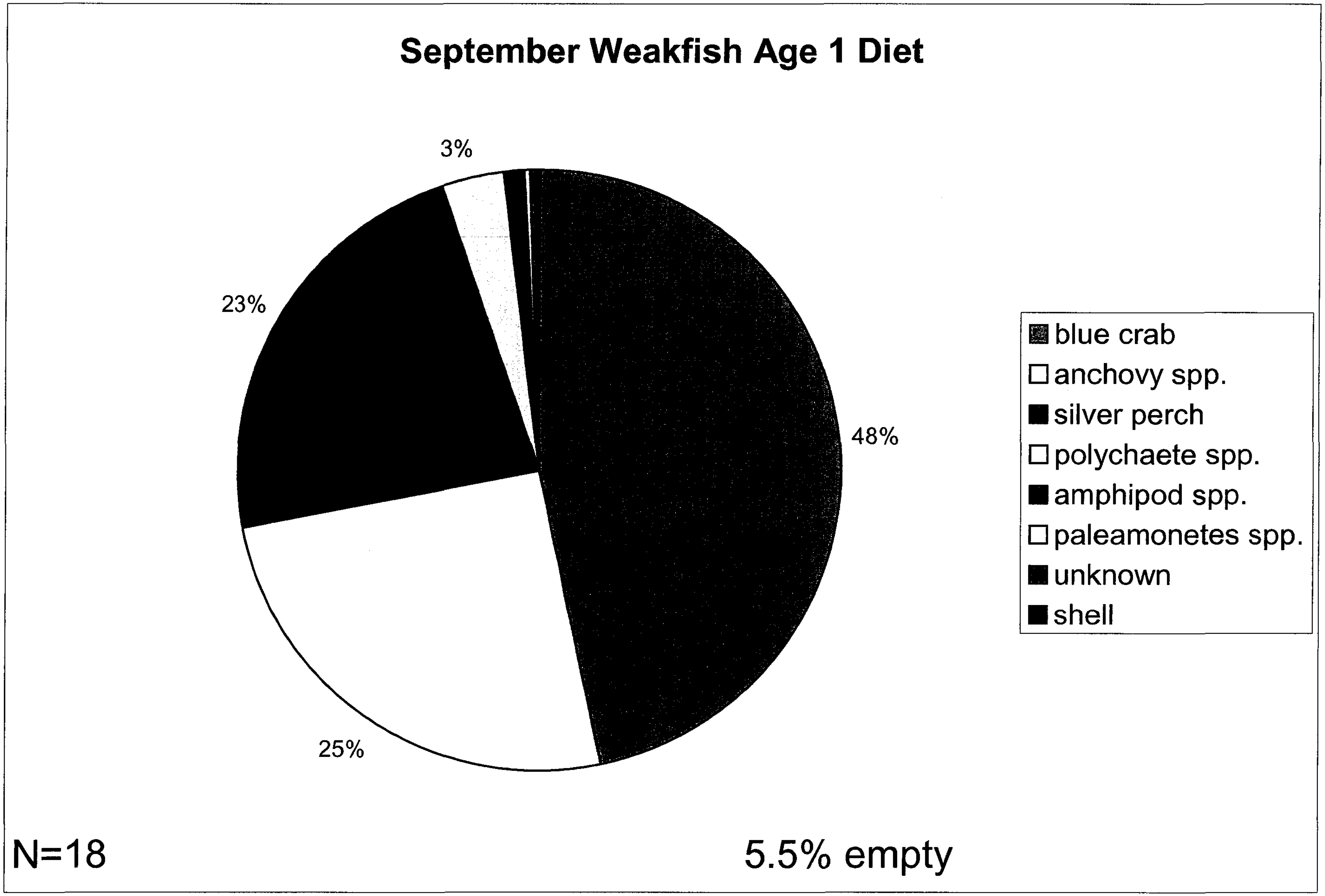
As in young striped bass (age1-3), blue crab made up the largest mass annually in age 1-3 weakfish. Diet diversity of age 1 fish was reduced in comparisons to age 2 and 3 fish. Reduced prey diversity was likely an artifact due to reduced age 1 abundances. Age 1 weakfish often contained prey of both benthic and pelagic trophic origins. In fact 58% of the stomachs examined contained a mixture of anchovy spp. and crustaceans. Anchovy spp. were so important to age 1 weakfish that when pelagic species were consumed alone (16%) stomachs contained anchovy only. Blue crabs were 34% of age 1 diet annually. Finfish of notable importance were silver perch (32%), anchovy spp. (20%) and spot (5%)(Fig. 3.37). Age 1 fish occurred in such small numbers in May that minimum sample size was not met. In June, abundance remained low (n=3) and the finfish spot (44%) and anchovy spp. (30%) dominated diet. Remaining mass was made up of smaller crustaceans including mysid spp. (12%), amphipod spp. (8%), and paleamonetes spp. (6%) (Fig. 3.38). After June, age 1 abundance remained too low for meaningful analysis until September. In September, blue crab (48%) was most important by mass. Anchovy spp. (25%) replaced spot as the dominant finfish followed closely by silver perch (23%). Amphipod and paleamonetes (1% combined) continued to appear in stomachs but relative mass was greatly reduced (Fig. 3.39).

Figures 3.37-3.39. These figures contain pie charts of age 1 weakfish. Annual content is presented first followed by monthly analysis in order sampled.


Weakfish Age 1 Annual
34%
32%
20%
5%
4%
2%
blue crab
silver perch
anchovy spp.
spot
unknown fish
polychaete spp.
amphipods
mysid
paleomonetes
unknown
shell
juv shrimp

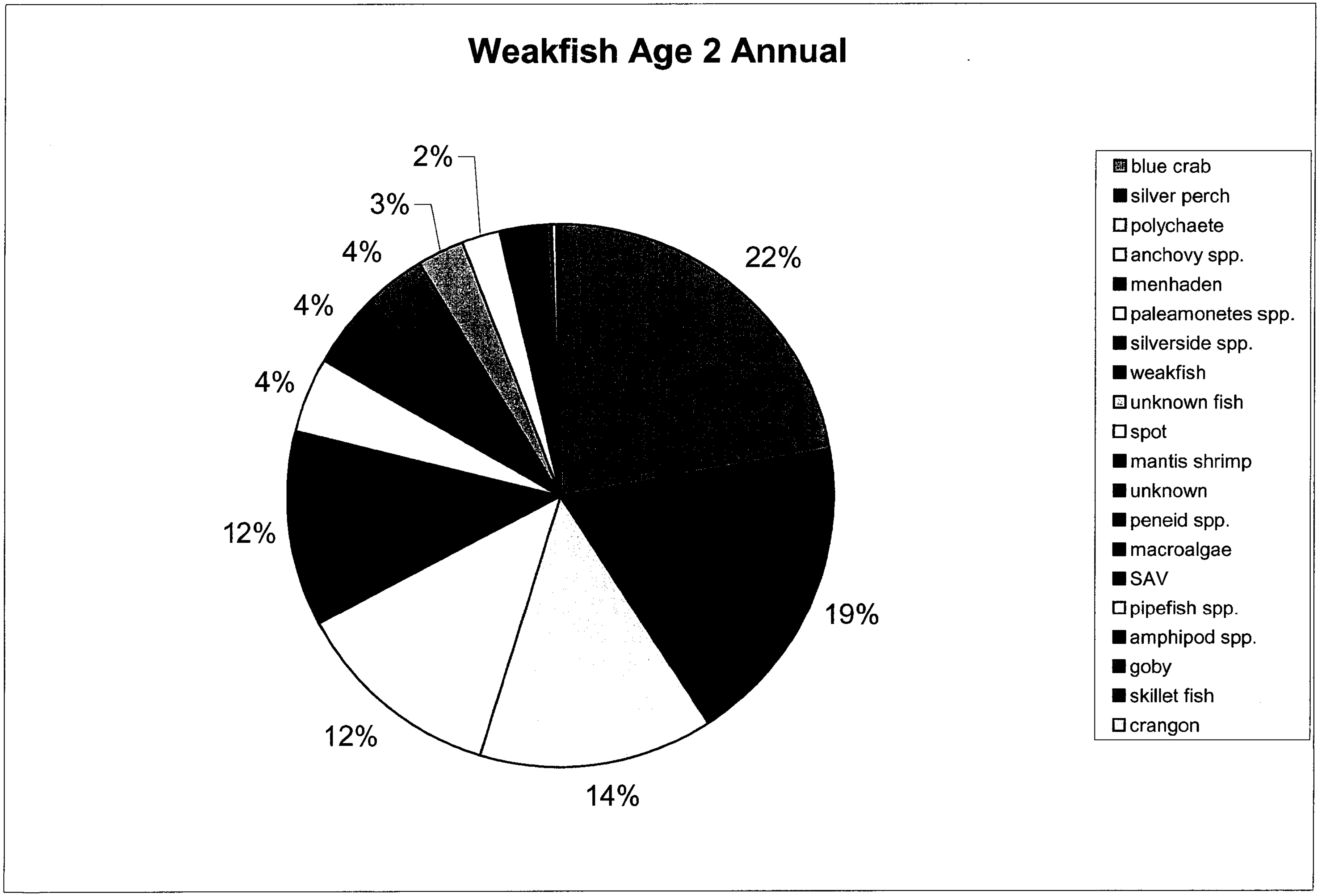


June Weakfish Age 1 Diet

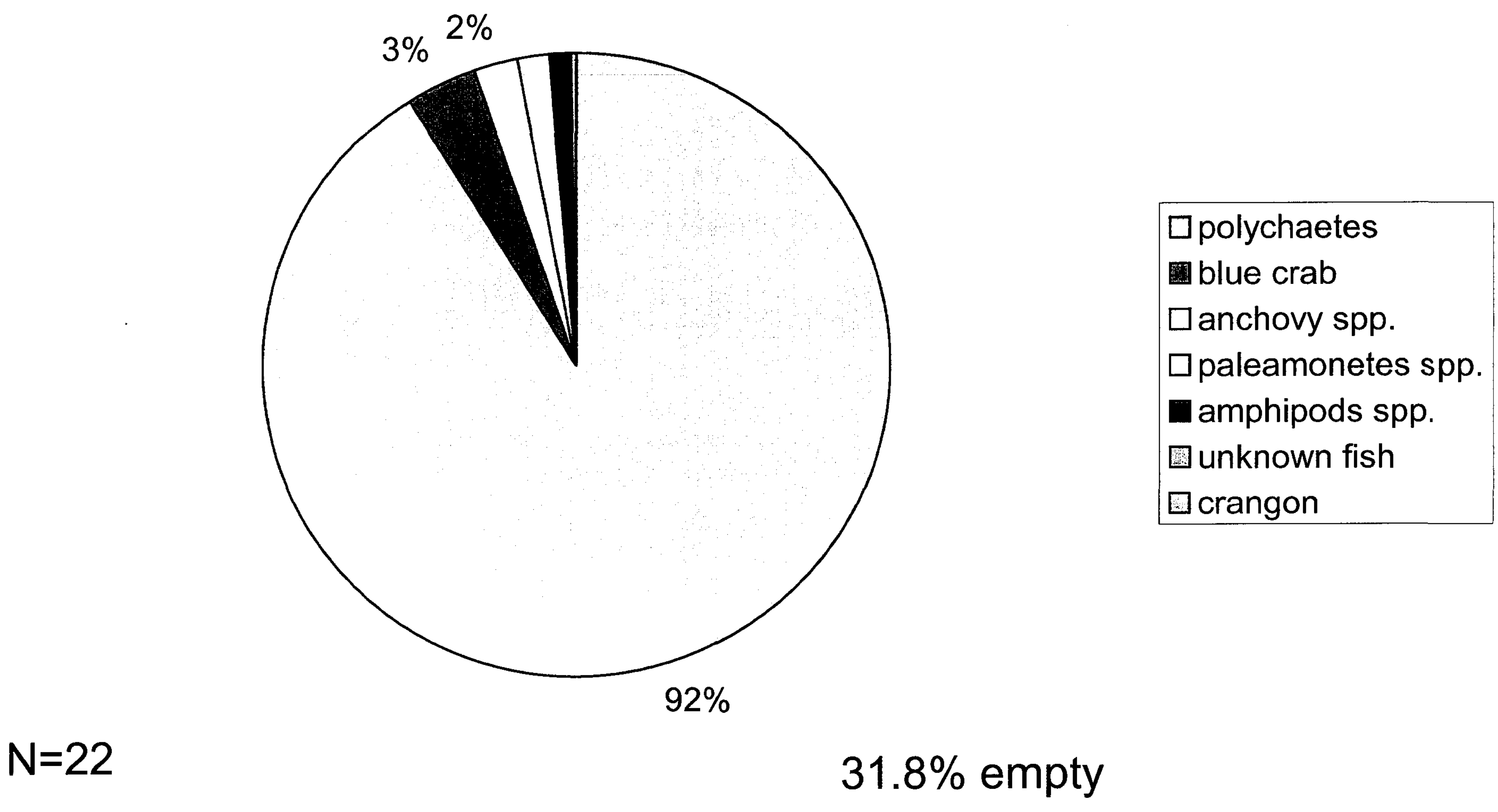

September Weakfish Age 1 Diet
3%
23%
48%
25%
blue crab
anchovy spp.
silver perch
polychaete spp.
amphipod spp.
paleamonetes spp.
unknown
shell
N=18
5.5% empty

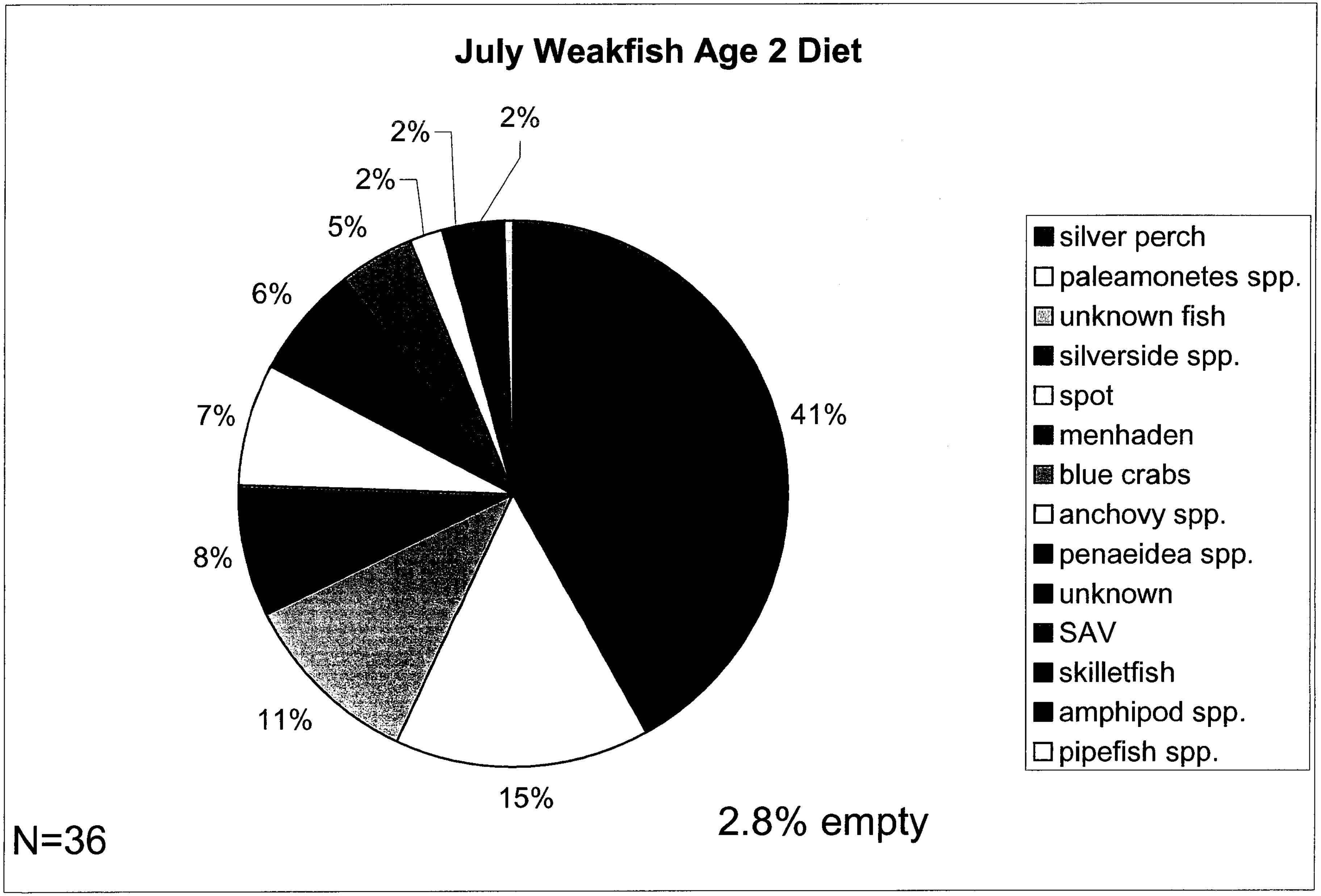
Age 2 diet diversity (n=20 items) increased relative to age 1 (n=12), but sample size was considerably larger (n=30 vs. 188). Age 2 weakfish and age 1 bluefish had the greatest diet breadths of the study each consuming an equal variety of prey items, again diet diversity may in part be due to increased sample sizes of these fish (See appendix 13). Age 2 weakfish gut contained both benthic and pelagic prey items less often then age 1 weakfish (32 vs. 58%) but showed greater elasticity in foraging strategies than age 2 bluefish or striped bass, whose gut never contained benthic and pelagic species mixed. Menhaden became a more important pelagic prey item in age 2 weakfish but stomachs that contained both benthic and pelagic prey most often contained anchovy or silverside spp. rather than menhaden. Annually, blue crabs (22%) were less important to age 2 weakfish than age 1 (34%), however, polychaetes spp. (14%) were much more important (Fig. 3.40). Silver perch (19%), menhaden (12%) and anchovy spp. (12%) were the most notable finfish. Percentage of finfish in age 1 (57%) and 2 fish (53%) remained relatively stable annually as did the dominant finfish species in diet (silver perch and anchovy). Age 2 finfish diet was twice as diverse as age 1. Menhaden were absent from age 1 diet but were important to age 2 fish. Age 2 fish also consumed silverside spp. and other weakfish species that were also absent from age 1 diet. Also a first, age 2 weakfish were the youngest fish of any species to consume mantis shrimp and the only group that contained any penaeid species. Age 2 diet in May was overwhelmingly dominated by polychaete spp. (92%)(Fig. 3.41). The vast majority of age 2 weakfish in May were collected on the 10th and polychaete spp. (predominantly *Nerius*) were notably important to all

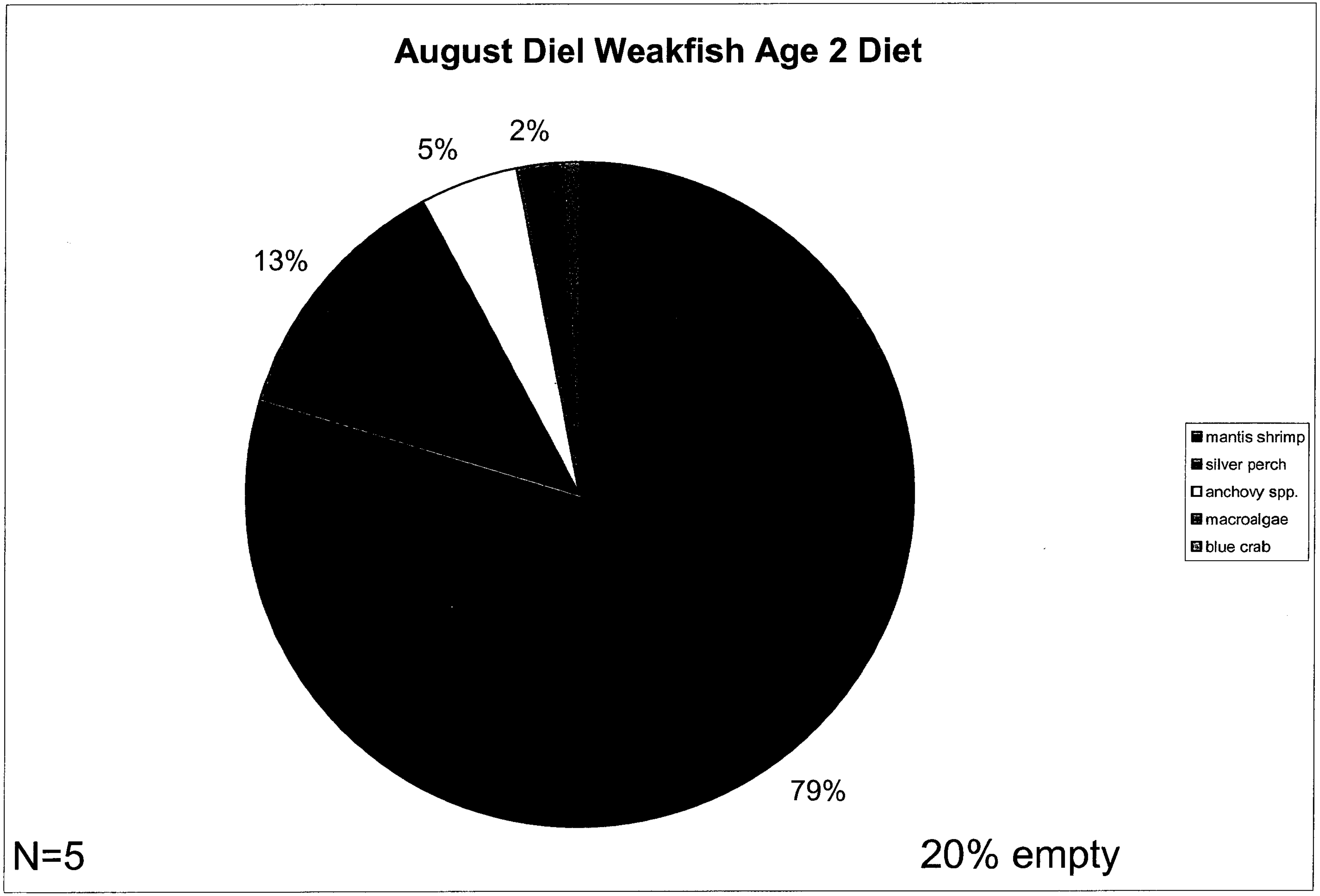
Figures 3.40-3.46. These figures contain pie charts of age 2 weakfish. Annual content is presented first followed by monthly analysis in order sampled.

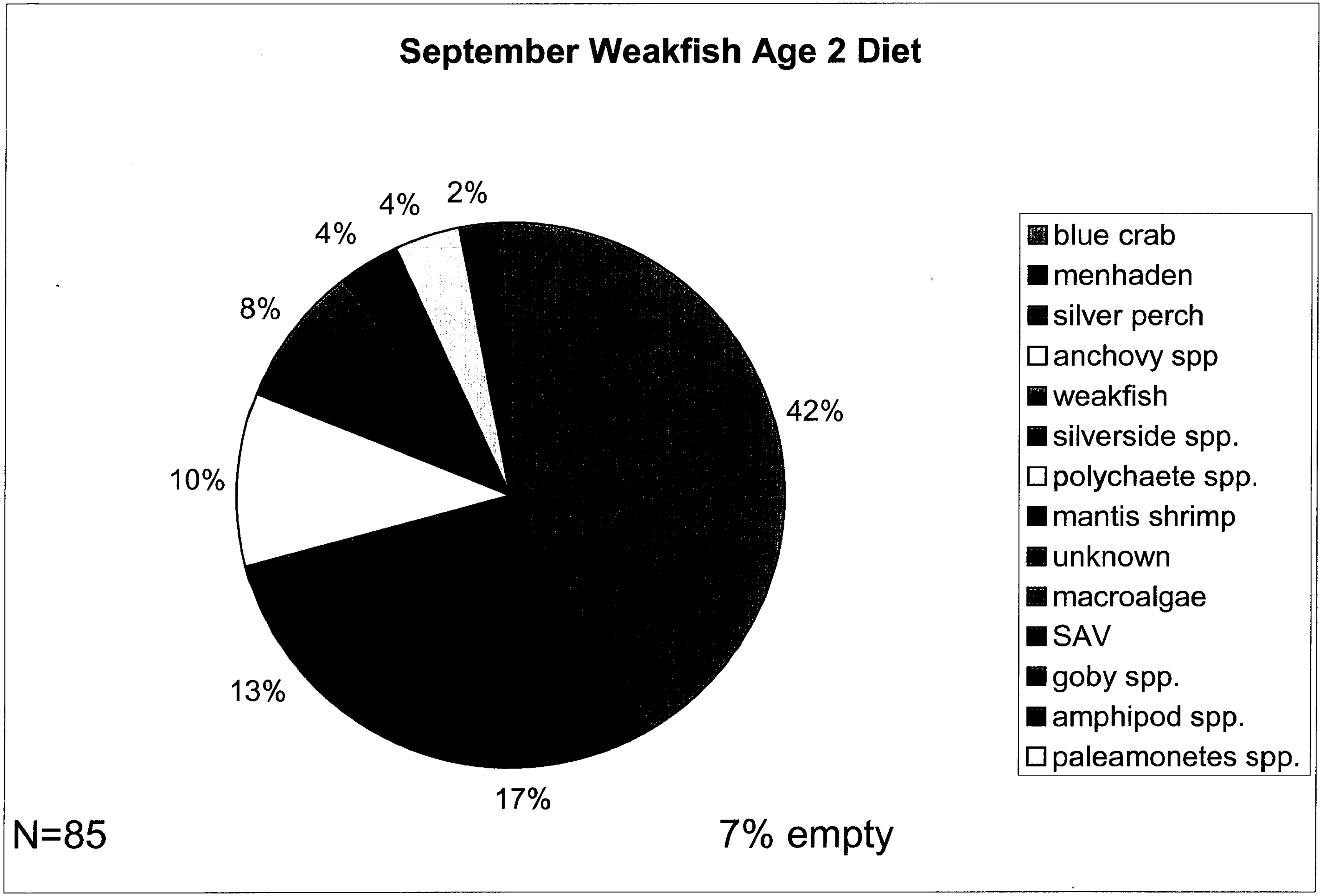

Weakfish Age 2 Annual
22%
19%
14%
12%
12%
4%
4%
4%
3%
2%
▨ blue crab
■ silver perch
☐ polychaete
☐ anchovy spp.
■ menhaden
☐ paleamonetes spp.
■ silverside spp.
■ weakfish
▨ unknown fish
☐ spot
■ mantis shrimp
■ unknown
■ peneid spp.
■ macroalgae
■ SAV
☐ pipefish spp.
■ amphipod spp.
■ goby
■ skillet fish
☐ crangon

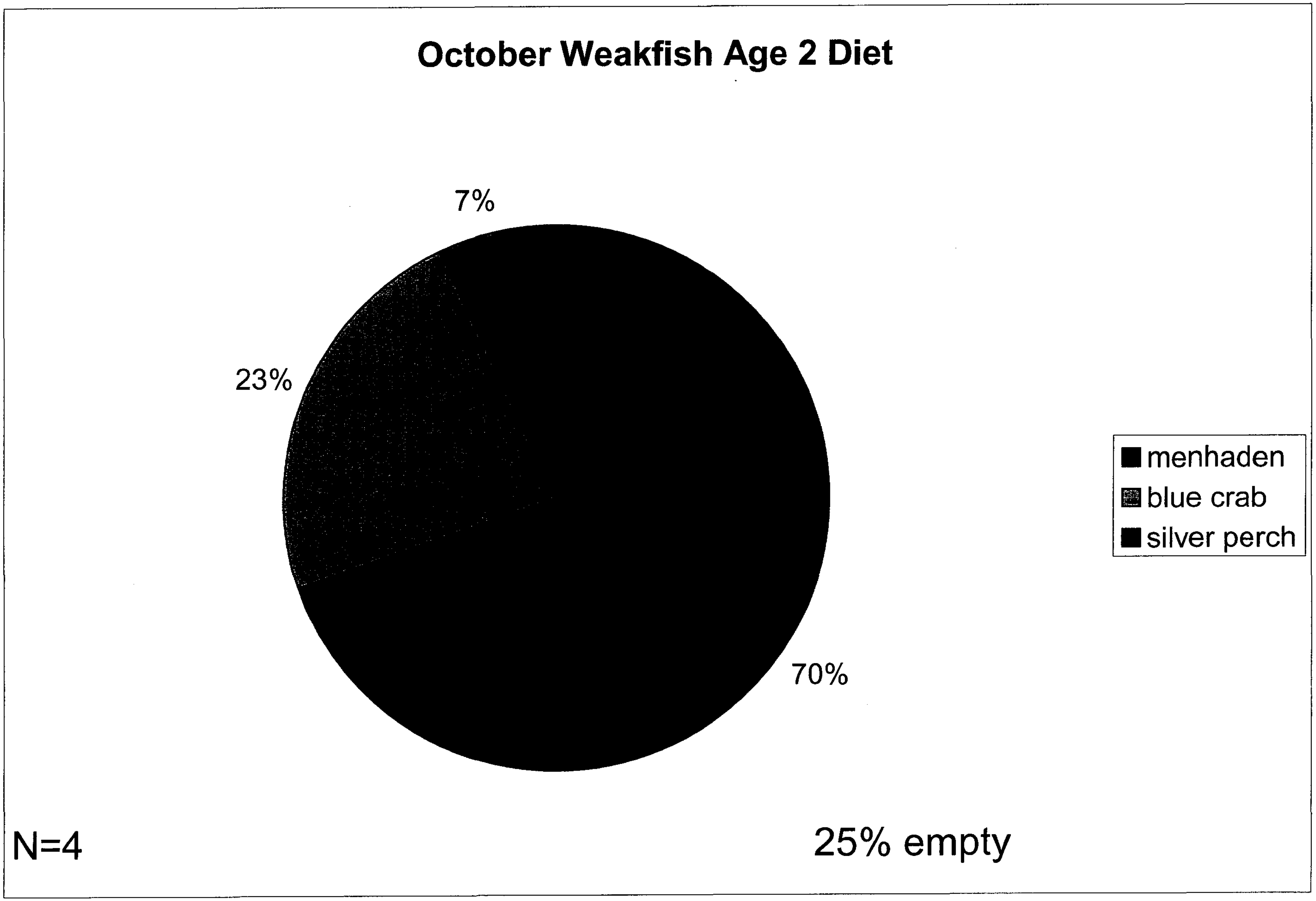
May Weakfish Age 2 Diet

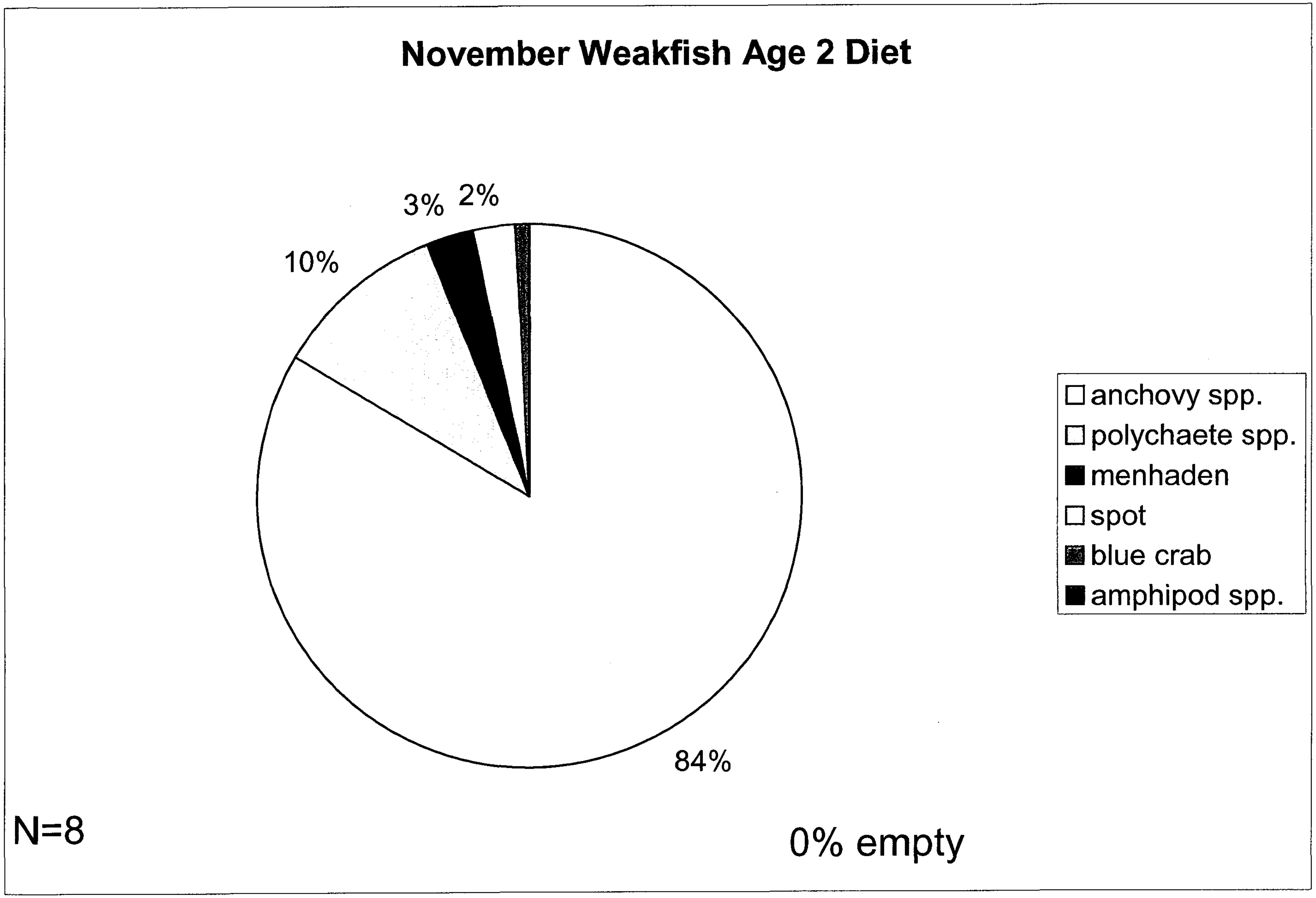



July Weakfish Age 2 Diet
2%
2%
2%
5%
6%
7%
8%
11%
15%
41%
silver perch
paleamonetes spp.
unknown fish
silverside spp.
spot
menhaden
blue crabs
anchovy spp.
penaeidea spp.
unknown
SAV
skilletfish
amphipod spp.
pipefish spp.
2.8% empty
N=36


August Diel Weakfish Age 2 Diet
2%
5%
13%
79%
■ mantis shrimp
■ silver perch
☐ anchovy spp.
▨ macroalgae
▨ blue crab
N=5
20% empty


September Weakfish Age 2 Diet
2%
4%
4%
8%
42%
10%
13%
17%
blue crab
menhaden
silver perch
anchovy spp
weakfish
silverside spp.
polychaete spp.
mantis shrimp
unknown
macroalgae
SAV
goby spp.
amphipod spp.
paleamonetes spp.
N=85
7% empty


October Weakfish Age 2 Diet
7%
23%
70%
■ menhaden
▨ blue crab
■ silver perch
N=4
25% empty

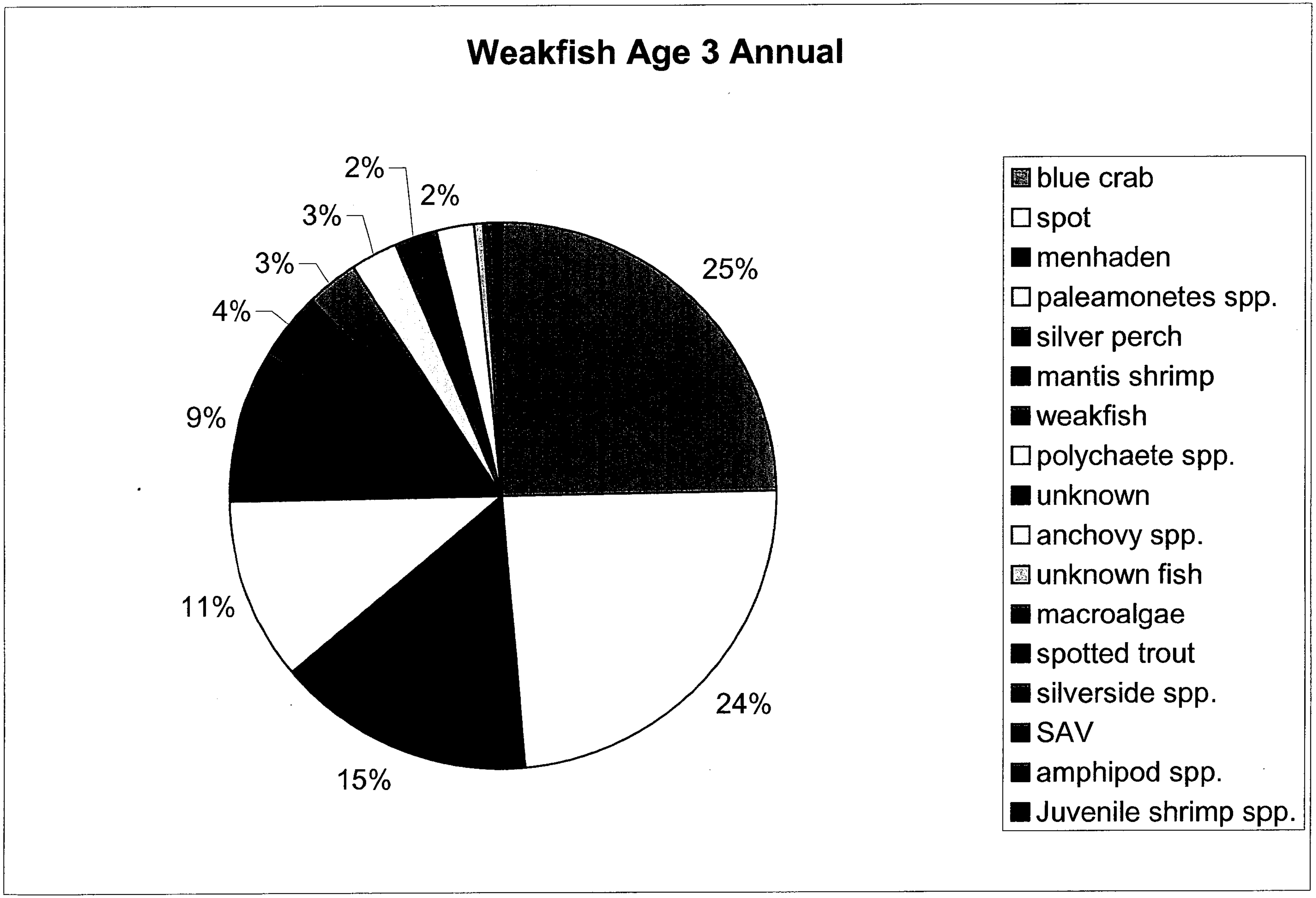

November Weakfish Age 2 Diet
10%
3%
2%
84%
☐ anchovy spp.
☐ polychaete spp.
■ menhaden
☐ spot
▨ blue crab
■ amphipod spp.
N=8
0% empty

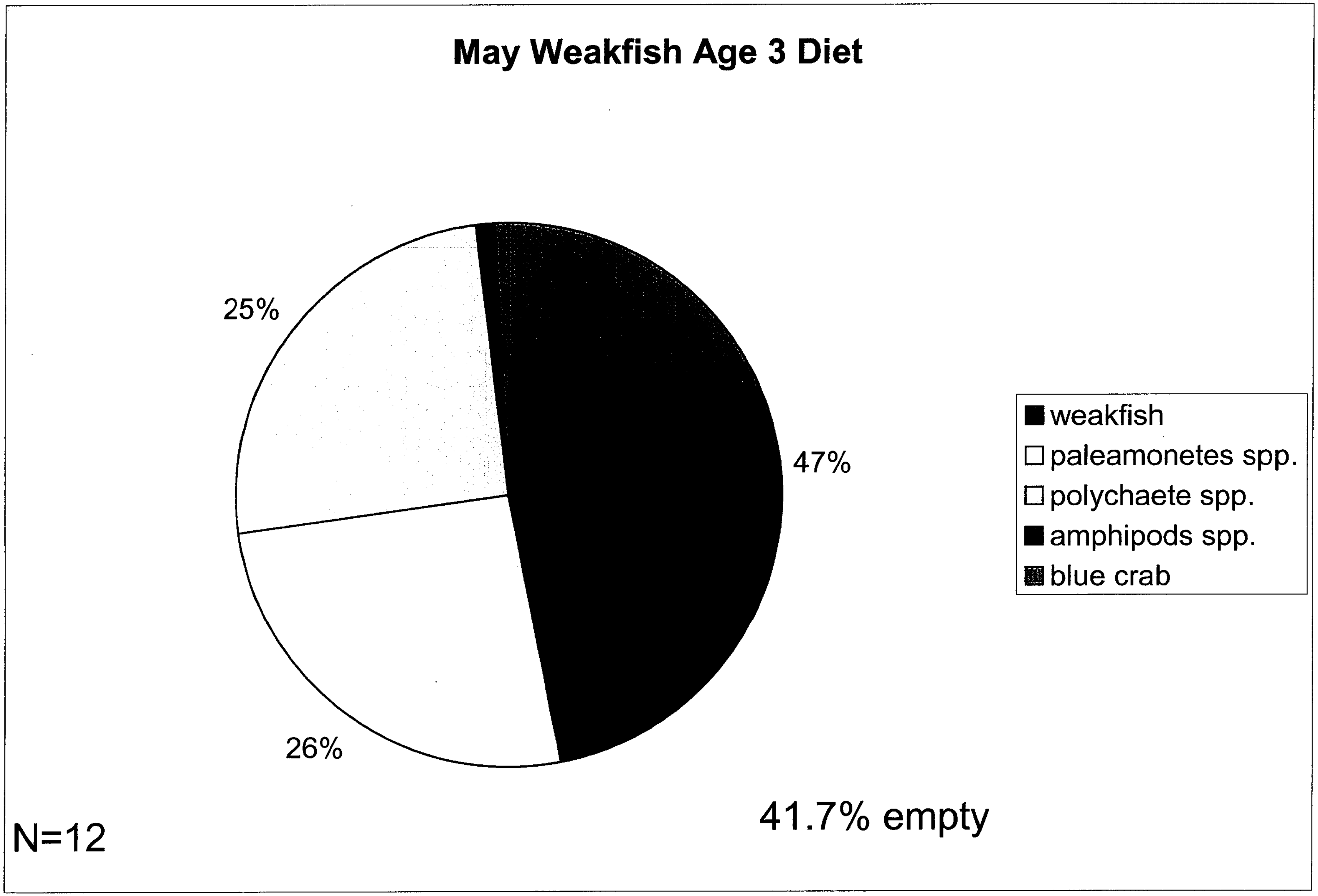
piscivores across age classes on this date. Very few (n=2) age 2 fish were sampled in June. In July, large numbers occurred. As in age 2 striped bass, and age 1 bluefish the importance of finfish particularly, silver perch (41%) and silverside spp. (8%), increased markedly in July (64%) as did the abundances of these prey species (Fig. 3.42, Table 2.3). The diel sample attained in August contained characteristically low numbers of fish (n=5) (Fig. 3.43). Mantis shrimp were the mass dominant (79%) followed by silver perch (13%) and anchovy spp. (5%). September samples were the largest of the study period (n=85). Diet was dominated by blue crab (42%) and total contributions by finfish were reduced (52%)(Fig. 3.44). Menhaden (17%) silver perch (13%), anchovy spp. (10%) and weakfish (8%) were notable finfish. Mantis shrimp were also eaten. October age 2 samples were greatly reduced (n=4). The majority of diet mass was menhaden (70%) followed by blue crab (23%) and silver perch (7%)(Fig. 3.45). November samples were twice that of October and may reflect a more robust sample of fall diet. Anchovy spp. vastly dominated diet (84%). Polychaetes were second (10%)(Fig. 3.46).

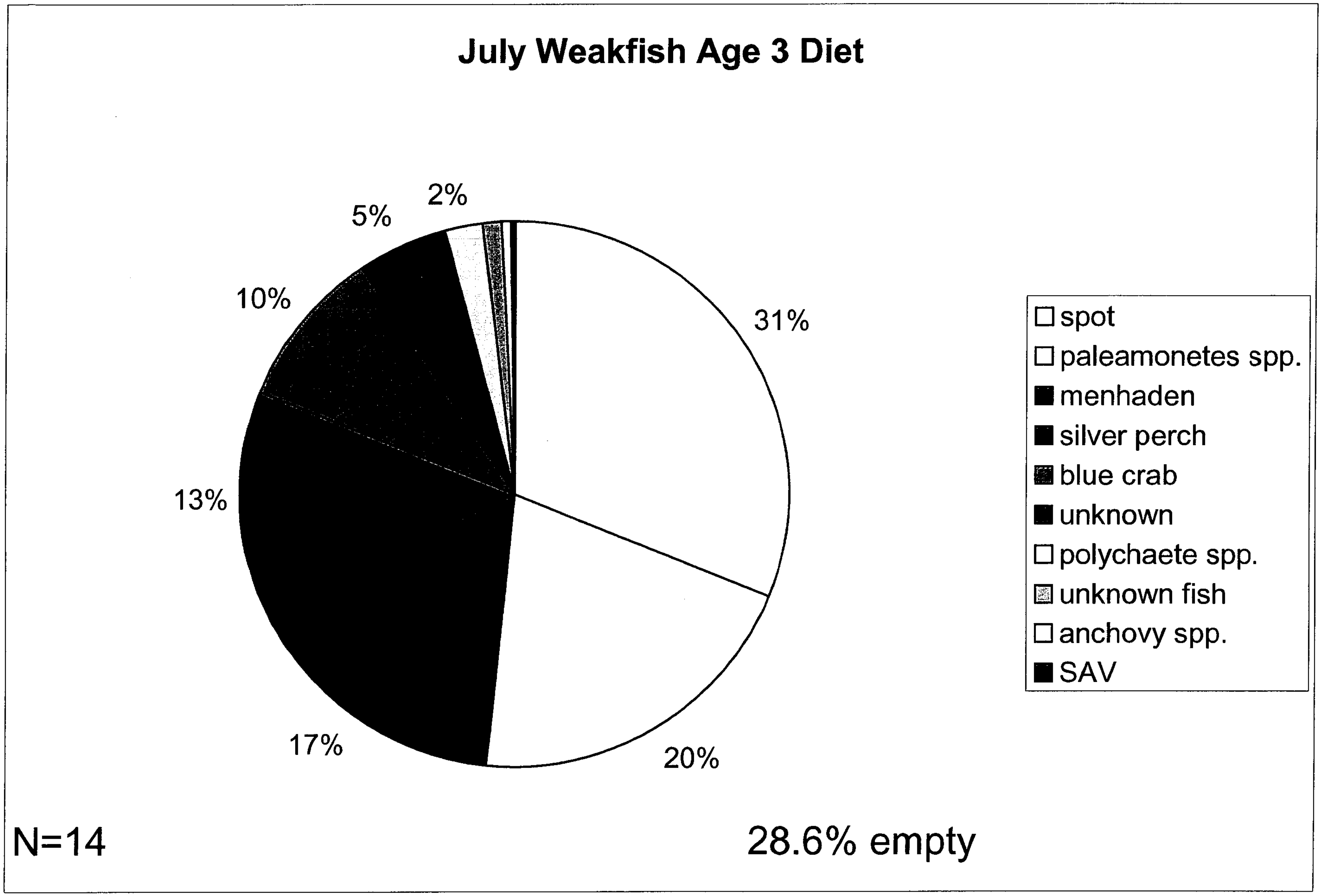
Though the number of age 3 weakfish collected was much less than that of age 2 (65 vs. 188) diet was almost as diverse (n=17 items). Sixty percent of age 3 fish contained benthic prey only and 20% contained both benthic and pelagic prey. Menhaden was increasingly important to age 3 fish relative to age 2 (15 vs. 12%) and in contrast to age 2 stomachs in age 3 fish gut menhaden commonly occurred along side benthic prey items predominantly blue crab. Annually blue crab was the dominant prey by mass (25%). Relative mass of blue crab was slightly greater than that found for age 2 fish (22%). Relative finfish mass was identical (53%) for age 2 and 3 fish, however, dominant finfish prey species changed. While age 2 finfish diet was dominated by silver perch (18%), menhaden (13%) and anchovy spp. (10%); age 3 diet consisted of spot (21%), menhaden (16%), and silver perch (9%) (Fig.3.47). May diet was dominated by weakfish (47%) and paleamonetes spp. (26%). Again polychaetes (25%) were found at their largest relative seasonal mass (Fig. 3.48). As was the case with age 2 fish June age 3 weakfish samples did not meet minimum sample number. July age 2 diet like age 2 striped bass, age 1 bluefish, and age 2 weakfish contained an increased prevalence of finfish. Finfish prey diversity (n=4 vs. 1) and quantity (62% vs. 47% in May) both increased in comparison to May. Silverside spp., which had been so important to other previously mention fishes, were noticeably absent (Fig. 3.49). Diet mass was dominated by larger spot (31%), menhaden (17%), and silver perch (13%). Crustacean (paleamonetes spp., 20% and blue crab, 10%) contributions were also significant. Large crustaceans (blue crab, 41% and mantis shrimp, 8%) were most important to age 3 fish in September (Fig. 3.50). Consequently, the combined contributions of finfish declined from 62% in July to 49% in September.

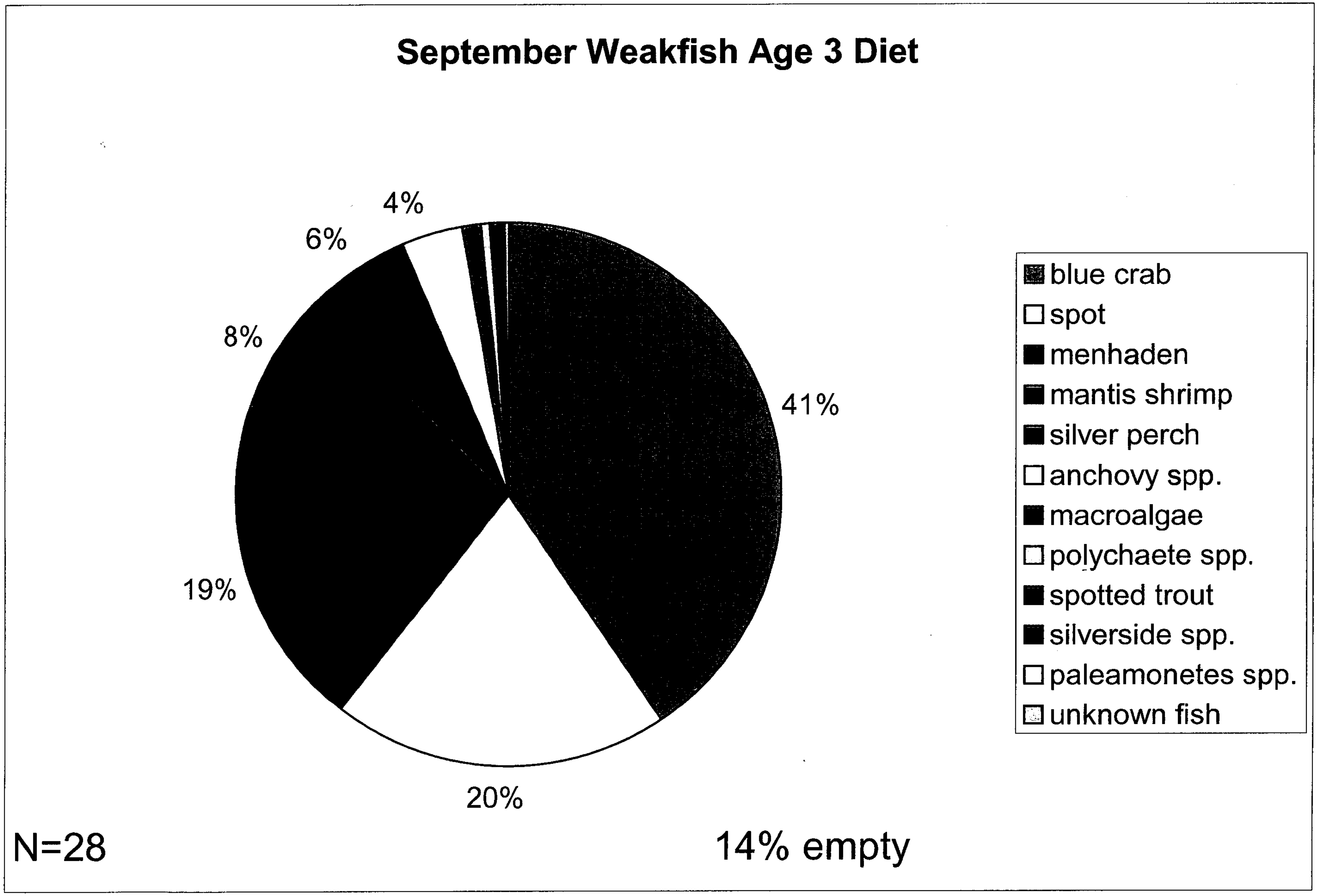
Weakfish age 3< were much less abundant (n=12) than other weakfish age classes (Appendix 13). Though blue crab occurred in the diet (20%), this age group's diet mass was dominated by finfish (67%) in particular menhaden. Fifty percent of stomachs examined contained benthic prey alone, and 25% contained both prey categories. Menhaden (37%) was by far the mass dominant followed by weakfish

Figures 3.47-3.50. These figures contain pie charts of age 3 weakfish. Annual content is presented first followed by monthly analysis in order sampled.


Weakfish Age 3 Annual
25%
24%
15%
11%
9%
4%
3%
3%
2%
2%
▨ blue crab
☐ spot
■ menhaden
☐ paleamonetes spp.
■ silver perch
■ mantis shrimp
■ weakfish
☐ polychaete spp.
■ unknown
☐ anchovy spp.
▨ unknown fish
■ macroalgae
■ spotted trout
■ silverside spp.
■ SAV
■ amphipod spp.
■ Juvenile shrimp spp.


May Weakfish Age 3 Diet
25%
47%
26%
■ weakfish
☐ paleamonetes spp.
☐ polychaete spp.
■ amphipods spp.
▨ blue crab
41.7% empty
N=12


July Weakfish Age 3 Diet
2%
5%
10%
31%
13%
17%
20%
spot
paleamonetes spp.
menhaden
silver perch
blue crab
unknown
polychaete spp.
unknown fish
anchovy spp.
SAV
N=14
28.6% empty


September Weakfish Age 3 Diet
4%
6%
8%
41%
19%
20%
blue crab
spot
menhaden
mantis shrimp
silver perch
anchovy spp.
macroalgae
polychaete spp.
spotted trout
silverside spp.
paleamonetes spp.
unknown fish
N=28
14% empty

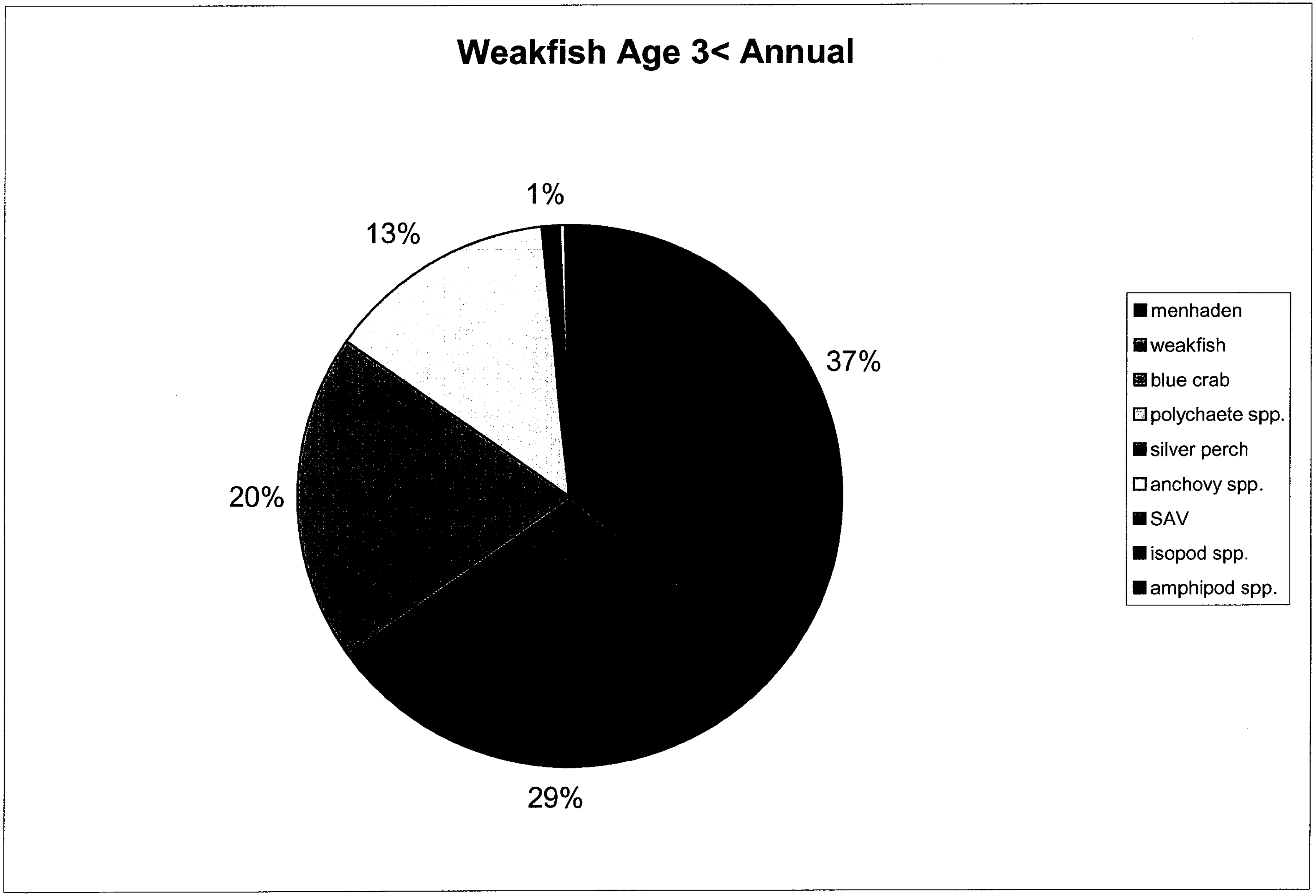
(30%) and both of these pelagic finfish occurred along side blue crabs in the gut. Polychaete spp. (13%) were again important, though their importance may be biased by a much greater abundance of fish of the age class during early May (Fig. 3.51). Unfortunately, age 3+ weakfish only occurred during two months in large enough numbers to warrant comparisons. May diet was dominated by menhaden (52%) and blue crab (27%) followed by polychaetes (19%)(Fig. 3.52). September sample size (n=3) was half that of May. Diet mass was composed of weakfish overwhelmingly (98%)(Fig. 3.53).

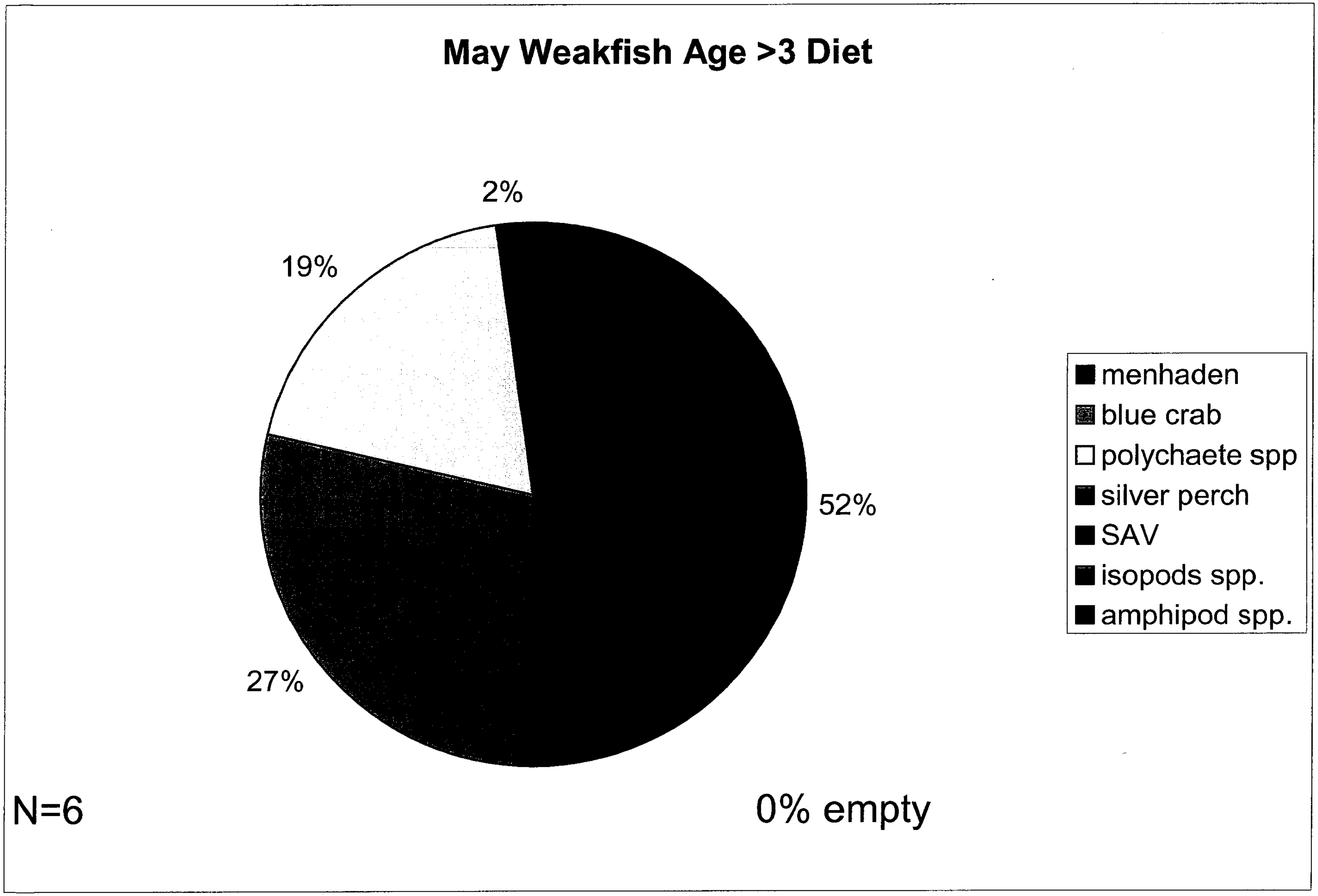
Trophic Ecology

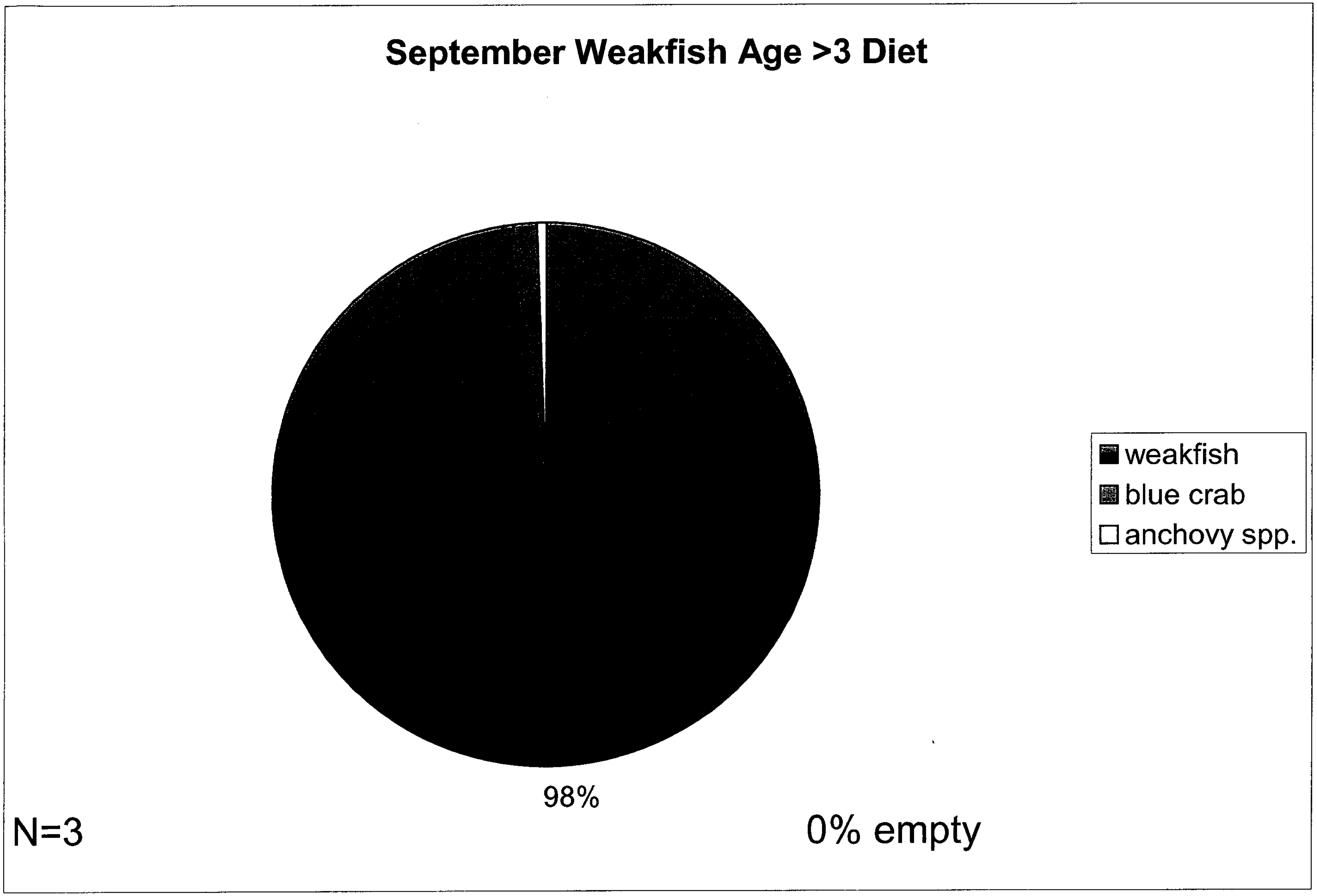
Stomachs often contained items that did not fit into either the benthic or pelagic prey categories; therefore, the percentage sum of the two may not be 100%. Graphs only contain nocturnal samples where number of stomachs examined equaled or exceeded 3 and more than one sample meeting this criteria occurred during the study period. Only nocturnal samples were consistently large enough to provide seasonal comparisons so diel samples were omitted. Benthic percentages are presented alone for clarity. Age specific percentages of benthic, pelagic, and other for all species and samples can be seen in Appendix 15.

No significant striped bass samples occurred during September, thus the trophic ecology graph appears broken across age classes. Age 1 striped bass show little variability in trophic ecology of prey. Benthic prey resources dominated the

Figures 3.51-3.53. These figures contain pie charts of age > 3 weakfish. Annual content is presented first followed by monthly analysis in order sampled.


Weakfish Age 3< Annual
1%
13%
37%
20%
29%
■ menhaden
■ weakfish
▨ blue crab
☐ polychaete spp.
■ silver perch
☐ anchovy spp.
■ SAV
■ isopod spp.
■ amphipod spp.


May Weakfish Age >3 Diet
2%
19%
52%
27%
■ menhaden
▨ blue crab
□ polychaete spp
■ silver perch
■ SAV
■ isopods spp.
■ amphipod spp.
N=6
0% empty


September Weakfish Age >3 Diet

diets of striped bass ages 1-3 throughout the study period (Fig. 3.54). Adequate samples of fish age > 4 were only collected in the fall (October-November) and the importance of pelagic species generally increased during the fall. Diets across age classes suggest an increased reliance on pelagic resources in the fall. Variability in trophic ecology of prey increased with age for striped bass. The trophic ecology of prey of age 1 bluefish was the most trophically dynamic of any age 1 fish. Though it was benthically dominated throughout the study period (Fig. 3.55) pelagic content increased steadily until mid-summer then returned to benthic dominance as fall approached. Age 2 bluefish diet was less dynamic and very different from age 1 fish in content. Age 2 diet consistently contained a greater mass of pelagic prey items than any other piscivore at any age (Appendix 15). Age 1 weakfish diet was not trophically dynamic; it consisted of relatively the same proportions of each prey category with benthic species clearly dominating mass (Fig. 3.56). Unfortunately, no late fall samples were available so analysis of seasonal shifts is limited. Age 2 weakfish samples were collected from across all seasons and illustrate a consistently increasing dependence on pelagic sources. Interestingly, age 3 weakfish showed an opposite trend with benthic resources increasing in relative mass. No fall samples of adequate size were collected for age 3 fish so it is unclear if this trend would have increased. Diet of fish > age 3 was consistently pelagically dominated but an increased reliance is evidenced in the late summer early fall. Across species age 1 fish were characterized by less seasonal variability in diet than other age classes and in general an increased annual reliance on benthic prey. In general, fish age 2 and

Figures 3.54-3.56. The seasonal trophic ecology of prey consumed by striped bass, bluefish, and weakfish is graphically displayed in the charts below. Stomach sample sizes of less than 3 and single samples of age groups were not included. Only benthic diet proportions are graphed. Exact percentages of pelagic and other can be seen in appendix 15.

Fig. 3.54

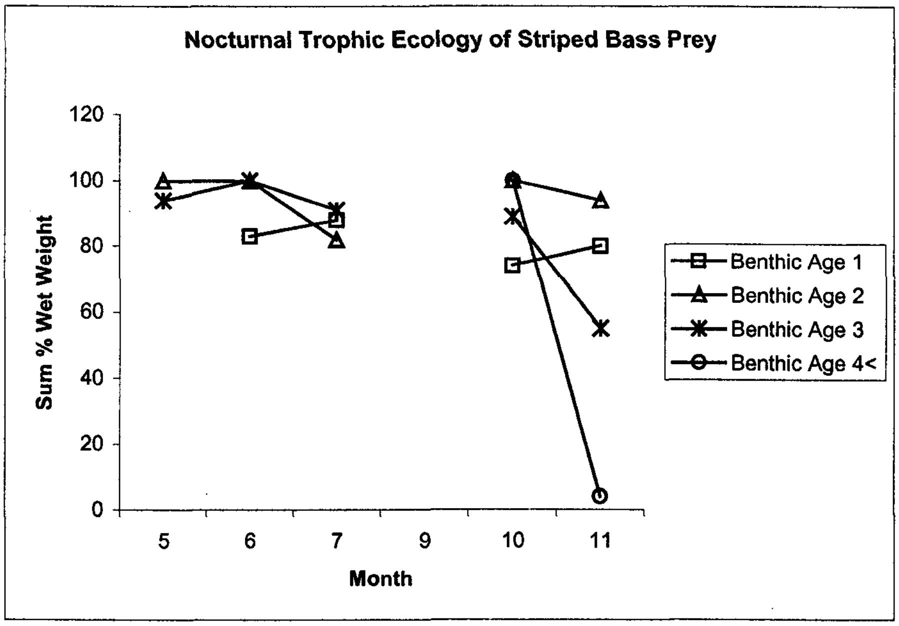


Fig. 3.55

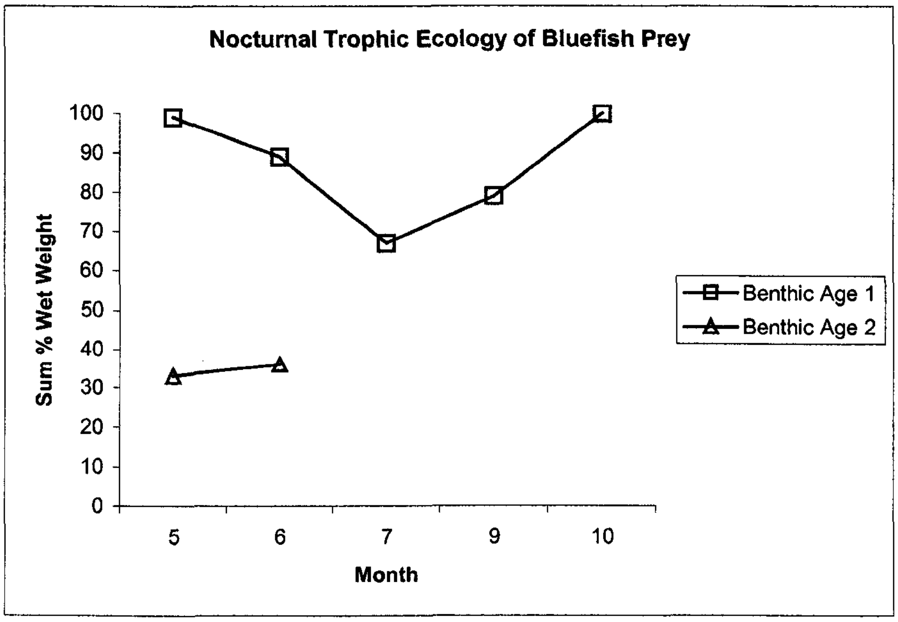
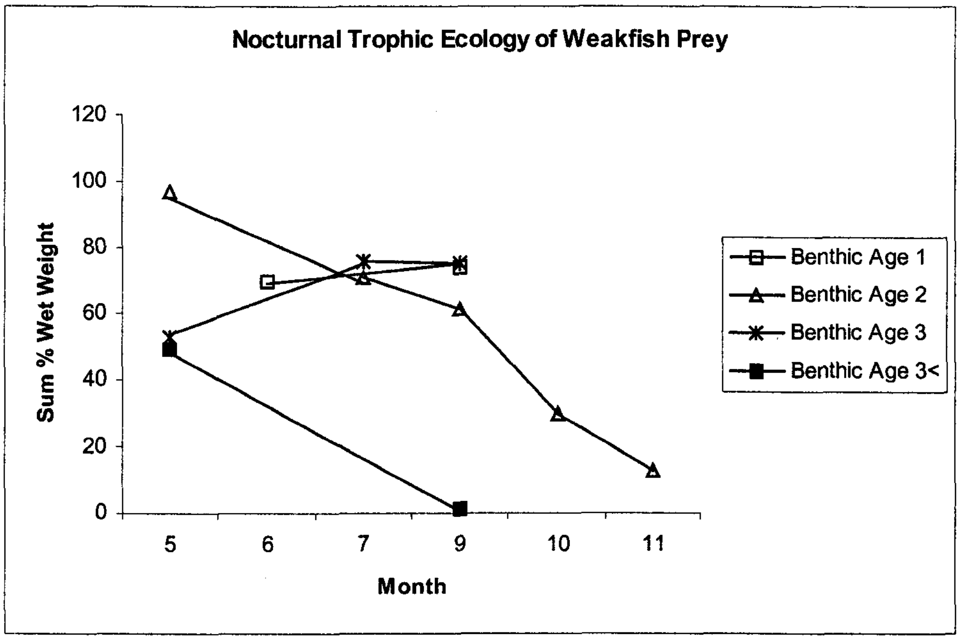


Fig. 3.56


Nocturnal Trophic Ecology of Weakfish Prey
Sum % Wet Weight
120
100
80
60
40
20
0
5
6
7
9
10
11
Month
Benthic Age 1
Benthic Age 2
Benthic Age 3
Benthic Age 3<

greater increased use of pelagic prey in the fall and reliance on pelagic sources (clupeids) increased with age.

Index of dietary overlap

Schoener's indices of dietary overlap were computed based on monthly mass percentages of prey across all ages of piscivores in order to compare the overlap between species. This resulted in 18 different indices (Fig. 3.57), three for each month sampled. Only one of these indices was above 60%. The September diets of weakfish and bluefish overlap by 69%. If an index > 50% is considered significant as in Hartman (1993) then weakfish and bluefish diets overlap significantly May-September. Inadequate bluefish abundance and subsequently poor diet data is likely the cause for low overlap indices in October and November. It is interesting to note that greatest dietary overlap across species and ages occurred in the fall preceding emigration concurrent with largest prey diversity and predator dietary diversity.

A total of 111 comparisons were made across sampled dates and age groups (Figure 3.58). Fourteen indices exceeded the 60% level. All species had an equal number of significant overlap values between species (n=4). Striped bass diets of age 2 overlapped with age 3 weakfish and age 3 striped bass overlapped with age 1 bluefish in early May (10th). Age 1 striped bass and bluefish diets overlapped again in late July (25th) and age 2 striped bass and weakfish overlapped on the same date. During September no striped bass occurred in the study site. Overlap greater than 60% did occur between age 1 bluefish and age 3 weakfish on both September sample

Figure 3.57. Schoener's index of dietary overlap all ages pooled:

	May			June		
Species	Blue	Weakfish	Striped bass	Blue	Weakfish	Striped bass
Blue	.	58%	29%	.	56%	7%
Weakfish	.	.	48%	.	.	9%

	July			Sept.		
Species	Blue	Weakfish	Striped bass	Blue	Weakfish	Striped bass
Blue	.	53%	29%	.	69%	44%
Weakfish	.	.	29%	.	.	39%

	Oct.			Nov.		
Species	Blue	Weakfish	Striped bass	Blue	Weakfish	Striped bass
Blue	.	7%	19%	.	7%	2%
Weakfish	.	.	33%	.	.	3%

Figure 3.58. This figure contains the results of Schoener's dietary overlap index based on W% for each nocturnal sample. Only samples were stomach number examined was at least 3 were included. Exact number examined on each date can be found in previous pie charts. All unknown, floral, and inert dietary components were excluded. Diel samples were excluded due to low sample numbers and/or lack of comparisons on sample dates.

Schoener's index of dietary overlap:

10-May

	SB3	B1	B2	W2	W3	W3<
SB2	38%	38%	38%	16%	95%	28%
SB3	.	73%	19%	33%	28%	50%
B1	.	.	21%	33%	30%	52%
B2	.	.	.	16%	17%	29%
W2	.	.	.	.	29%	23%
W3	.	.	.	.	.	20%

25-May

	B2	W2
B1	5%	33%
B2	.	5%

12-Jun

	SB2	SB3	B1	B2	W1
SB1	21%	13%	35%	47%	23%
SB2	.	92%	10%	24%	36%
SB3	.	.	2%	16%	30%
B1	.	.	.	52%	8%
B2	.	.	.	.	22%

10-Jul

	SB2	B1	W2	W3
SB1	0.40%	7%	15%	23%
SB2	.	45%	4%	2%
B1	.	.	38%	30%
W2	.	.	.	57%

	25-Jul				
	SB2	SB3	B1	W2	W3
SB1	19%	6%	62%	48%	18%
SB2	.	51%	32%	64%	26%
SB3	.	.	5%	15%	9%
B1	.	.	.	59%	22%
W2	.	.	.	.	30%

	18-Sep		
	W1	W2	W3
B1	27%	18%	64%
W1	.	57%	42%
W2	.	.	41%

	25-Sep			
	W1	W2	W3	W3<
B1	51%	51%	75%	4%
W1	.	91%	58%	2%
W2	.	.	66%	3%
W3	.	.	.	3%

	9-Oct					
	SB2	SB3	SB4	SB4<	B1	W2
SB1	63%	51%	26%	49%	0	23%
SB2	.	79%	59%	68%	16%	31%
SB3	.	.	53%	61%	10%	33%
SB4	.	.	.	72%	57%	30%
SB4<	.	.	.	.	47%	30%
B1	.	.	.	.	.	7%

	19-Nov			
	SB2	SB3	SB4<	W2
SB1	7%	5%	4%	16%
SB2	.	9%	3%	14%
SB3	.	.	5%	5%
SB4<	.	.	.	0.08%

dates and between age 1 and 2 and age 2 and 3 weakfish in the later part of the month. Within species comparisons were most numerous for striped bass (n=6) and most of these (5) overlaps occurred during a single month (Oct.) when sample size was large and age structure diverse. In October, age 1 diet overlapped with age 2 and age 2 with age 3. The diet of striped bass 4< overlapped with age 2-4. An extremely high overlap also occurred between age 2 and 3 fish in June. Consistent overlap between species' age classes occurred within the same month only once (Sept., B1 vs. W3). Diet overlap exceeding 60% level between age 1 and 2 bluefish did not occur.

DISCUSSION

In comparisons with terrestrial ecologist, aquatic ecologist studying trophic interactions face logistic difficulties that largely prevent precise determination of acquisition location. Habitat specific marine diet studies are more likely, therefore, to be faced with the question: "How can one tell that the prey found in the gut originated in the system of capture when its actual capture was not witnessed?" In practice, guaranteeing that all prey was attained in a given marine habitat without restricting natural movement of both predator and prey is impossible. The likelihood that gut content was attained in vastly different habitats, however, can be minimized and thus the locational assumption of prey consumption strengthened by selecting an appropriate study site. The possibility of foreign gut content in this study was minimized by the large sample area within the site and its geographic location in the middle of littoral zones filled with similar habitats. Finding paleamonetes shrimp spp. a prey only found in littoral habitats in the gut of all fishes examined except 4 and 4< striped bass supports the principle assumption of trophic location acquisition. Every age class across species contained SAV and/or macroalgae except age 1 weakfish. True this flora could have been consumed outside of the site but an equally plausible explanation is that it was ingested accidentally while targeting prey hidden within. The study site and surrounding littoral zones contained a large amount of both types of habitats so this theory seems likely. The fresh state of the majority of prey items ingested further suggests that most prey were consumed on site.

Many previous Chesapeake Bay diet analysis of striped bass, bluefish, and weakfish have revealed a greater trophic dependence on pelagic rather than benthic prey items (Hollis, 1952; Chao and Musick, 1977; Lascara, 1981; Baird and Ulanowitz, 1989; Hartman and Brandt, 1995a, Overton et al. 2000; Overton, 2002; Walter and Austin, 2002; Griffin and Margraf, 2003). Baird and Ulanowitz (1989) estimated that 91-100% of the carbon flow that benefited striped bass and weakfish originated in the pelagic pathway. Hartman and Brandt (1995a) asserted that striped bass, bluefish, and weakfish production in the bay was the direct result of only a few pelagic prey items. Bay anchovy and menhaden supported most of the production of all three piscivores in their study. What is notable in the piscivore diets presented in these works is a lack of diet diversity and benthic prey especially invertebrates.

Benthic prey resources especially invertebrates were an important part of all piscivore diets in littoral habitats and would thus also be important to production within the zone. Diet diversity for all piscivores was much greater than that previously reported by the most recent study covering all three piscivores by Hartman and Brandt (1995a). Production would not be the product of a few overlapping prey items but would be the result of prey distributed more evenly across trophic pathways. Crustaceans dominated the diets of age 1-3 striped bass, age 1 bluefish, and age 1-3 weakfish. Diets of older fish though more diverse than those found by previous investigators generally contained a much larger proportion (%W) of pelagic species. In agreement with most previous works older larger age 4 and >4 striped bass, age 2 bluefish, and age >3 weakfish diets consisted primarily of finfish generally dominated by clupeiods. Striped bass stomachs were less likely to contain both benthic and pelagic prey species with age suggesting that feeding strategies become more specialized with age. Bluefish showed a clear preference for pelagic prey at younger age than other piscivores. In contrast to age 1 fish (21%) gut of age 2 fish never contained both types of prey. This may suggest that switching to a pelagic dominated diet required different more specialized feeding strategies that did not allow fish to take advantage of both benthic and pelagic prey simultaneously. Weakfish across ages contained a greater percentage of mixed benthic and pelagic prey items consistently. Increases in diet breadth within individual fish may be due to more elastic feeding strategies that allow the species to take advantage of various prey types, possibly in different habitats, over a relatively short period of time. This finding may indicate that weakfish occupy a feeding niche not capitalized on by other often-competing piscivores.

The dietary importance of crustaceans to YOY striped bass is well established (Bason, 1971; Cooper et al., 1998; de Sylva, 1962; Gardiner and Hoff, 1982; Hartman and Brandt, 1995a; Walter et al., 2003) across various habitats. In agreement, Hartman and Brandt (1995a) found that invertebrates were important to small (age-0) striped bass. No age 0 fish were analyzed in this study but invertebrates, particularly blue crabs, dominated littoral diet mass of age 1-3 striped bass. Seasonally blue crabs were even important to older fish (age 4 and > 4) thus in agreement with Walter and Austin (2003) benthic species were much more important to larger striped bass than in previous studies. Also in agreement was the increased importance of gizzard shad found in both studies. Recent analysis of striped bass diet collected from around oyster reefs and sand bars in the Piankatank River (Harding and Mann, 2003), just north of the sample site, also show a marked increase in benthic prey. Across all sites sampled benthic species were 94% of numerical abundance and 80% by frequency. Studies in other regions also suggest that the diets of striped bass are far more flexible (Dovel et al., 1968; Schaefer, 1970; Boynton et al., 1981; Schulze, 1996; Dunnig et al., 1997; Tupper and Able, 2000; Nelson, Chase and Stockwell, 2003) than the findings of Hartman and Brandt (1995a) would lead one to conclude. Striped bass sampled from salt marsh creeks in Delaware Bay were overwhelmingly dominated by crustacean species, containing blue crabs, grass shrimp, sand shrimp and mummichog (Tupper and Able, 2000; Nermerson and Able, 2003). Diet of age 1 fish sampled in the New York bight was also dominated by invertebrates (Buckel and McKown, 2002). Invertebrates are in general far more important to larger striped bass in northern sample sites from which most of this conflicting data was gathered; dietary discrepancies are generally explained by a proposed lack of pelagic prey in these regions (Walter et al., 2003). The findings of this study and Harding and Mann (2003) suggest that invertebrates are much more important to striped bass in specific habitats within the bay as well.

A consistent dependence of weakfish on pelagic prey is far from established. In fact, weakfish were much more likely to have both benthic and pelagic prey items mixed in their gut across all age classes examined (34% vs. 11 and 6% for bluefish and striped bass) than either other piscivore. A mid-summer study in the York River channel adjacent to the study site found that the importance of anchovy and mysid were nearly evenly split (Chao, 1976). Lascara (1981) studied weakfish diet in several littoral habitats in the Chesapeake. He sampled in and around littoral grass beds using gill nets from April-November along the lower Eastern Shore. Shrimp and crabs dominated weakfish diet in number and frequency. In surrounding sand flats, a greater dependence on fishes was found. Anchovy spp. increased in frequency for weakfish but shrimp remained dominant in abundance. Unfortunately, percent volume and/or percent weight were not calculated. Results, however, provide an example of the increased importance of crustacean prey in littoral sites. Diet studies from Albemarle Sound in North Carolina found that shrimp, anchovies and clupeid fish dominated weakfish diets (Linton, 1904; Welsh and Breder, 1923). As in this study, diet preferences switched from crustaceans to menhaden as fish grew (Welsh and Breder, 1923; Merriner, 1973). Grecay (1990) sampled from the middle of Delaware Bay and found that weakfish relied more heavily on macrozooplankton (mysid) than anchovy. Earlier, a seasonal study from June to September in the same area also found that macrozooplankton dominated diet until fall when fishes switched to a pelagic diet dominated by anchovy (Thomas, 1971). Across weakfish age classes there was a trend towards an increased importance of pelagic prey in the fall in this study as well.

The crustacean dominance of diet in age 1 bluefish in littoral zones was possibly the most surprising find of the study. Other studies have illustrated that pelagic prey often dominate gut content in age 0 (Buckel and Conover 1996, 1997, Buckel et al. 1999, Buckel and Mckown, 2002). A clear shift to pelagic (menhaden) prey was evidenced in age 2 fish. This finding agrees with that of Hartman and Brandt (1995a). Lascara (1981) analyzed bluefish diet congruently with the weakfish he collected along the Eastern Shore in 1980. During this time large bluefish that typically have a pelagically dominated diet were abundant in the Chesapeake. Though the bluefish he sampled averaged 450mm SL (age 2) they consumed a majority of shrimp by number. Menhaden, spot and mullet dominated frequency. In the surrounding sand flats, menhaden dominated bluefish diet in number and frequency. Though bluefish sampled by Lascara (1981) were on average older and larger than those sampled in this study, his results provide an example of how elastic bluefish diet can be and how much more important crustacean prey is in littoral habitats. Benthic species including shrimp spp. were also found to be more important to bluefish sampled around Piankatank River oyster and sandbars (Harding and Mann, 2001) than reported in previous works (Juanes and Conover, 1994a; Hartman and Brandt, 1995a; Buckel and Conover, 1997; Buckel et al., 1999b; Able et al., 2002). Across all sites benthic species were 64% numerically and 43% by frequency and a large number of shrimp spp. (18%N) were reported. When Baird and Ulanowitz (1989) cited an increased dependence upon benthic resources (based on 11 stomachs collected by Homer and Boynton, 1978) in comparison with that found by

Hartman and Brandt (1995a). Hartman and Brandt (1995a) at first suggested that low sample size was to blame. Habitat specific works suggest that bluefish gut content may vary significantly depending on season and/or habitat.

Most studies of piscivore gut content show an increase in reliance on pelagic pathways in the fall (Walsh and Breder, 1923; Thomas, 1971; Schwartz et al., 1980; Hartman and Brandt, 1995a). When age classes were pooled similar trends towards an increased pelagic importance in the fall were found in this study. Age specific examination of diet (W%) tells a very different story. Ontenogenic changes are known to affect diet composition. Relative mouth gape offers a simple explanation for diet restriction. Range of prey size increases with increased predator size and ratio based trophic niche breadths generally do not expand with ontogeny but tend to narrow for larger predators (Scharf et al., 2000). Dietary analysis of piscivore gut content in this study supported these findings.

Hartman and Brandt (1995a) found that in general pelagic prey sources dominate piscivore diets and production in the Chesapeake. Obvious age specific alterations in trophic ecology occurred seasonally in both studies but trophic ecological dependence and direction of alterations between studies are inconsistent. In their work, age 1 striped bass steadily increased their dependence on pelagic resources and by September they dominated diet. Age 1 fish increased their use of pelagic sources in this study in the fall but they never dominate diet mass. In early summer, age 2-3 fish in the upper bay (Hartman and Brandt, 1995a) sampled from an unknown habitat switched from a pelagic diet to a benthic one (80% or greater). Pelagic dominance returned in the fall. Age 2-3 fish increased use of pelagic prey (silverside spp.) in mid-summer in littoral habitats but even at this time diet remained overwhelmingly benthic in origin. In fact, age 2 and 3 fish were consistently more dependent on benthic prey items than age 1 fish. Interestingly, the diet age > 4 fish changed drastically between fall sample dates. It was benthically dominated in October (blue crab and silver perch) and by November the percentage of pelagic prey increased drastically. Smaller fish were more abundant in the October sample and blue crabs and silver perch were still available in the study site (Table 2.3). By November much larger fish had immigrated into the study site and the populations of blue crab and perch were greatly reduced. The increased mouth gape of the larger fish allowed them to take advantage of the plentiful gizzard shad in the site and the dominance of the fish in diets at the time reflects their consumption. Hartman and Brandt did not examine any fish over age 3 so comparisons cannot be made but Walter et al. (2003) found that gizzard shad are often consumed by larger striped bass in waters of lower salinity. Clear ontenogenic diet alterations were not evident. Littoral diet for all but the largest fish was consistently dominated by blue crab, which occurred in high densities (Table 2.3). The increased importance of this prey item in littoral zones suggests that in general striped bass were feeding on the most available prey based on abundance. Clear annual dominance of finfish prey was evident in age > 4 fish but annual diet was based on a relatively small number of fish sampled in the fall. Dominance of blue crab in age > 4 diet in October may suggest that there is a significant seasonal component affecting diet even in these much larger fish.

Bluefish trophic ecology tells a somewhat similar story in both studies. Hartman and Brandt (1995a) found that in general pelagic sources were dominant across age classes and that distinct seasonal shifts occurred in the diets of age 1 and 2 fish. Pelagic prey was more than 50% of diet portion when first sampled and reliance increased in the fall. Age based dietary differences were pronounced in their study. Age 1 fish showed an increased reliance on pelagic resources in mid-summer when pelagic species abundance (silverside spp.) was augmented but benthic resources clearly dominated diet throughout study period. Hartman and Brandt (1995a) found a relative increase in dependence of age 2 fish on benthic prey in late summer (July-Aug) and an increased pelagic role in fall (Sept- Oct.). Age 2 fish were only sampled in the spring in this study (May-June). Diet was dominated by pelagic sources (menhaden) in May but a reliance on benthic prey was noticed in (paleamonetes spp.) in June before they left the area. Growth rates of bluefish have been shown to be improved when based on a diet of fish verses crustaceans (Juanes and Conover, 1994b). It is possible that larger bluefish faced with the rising energetic cost associated with increasing water temperatures (Hartman and Brandt, 1995a) at first attempted to offset losses by capitalizing on more abundant crustacean prey but eventually emigrated from the area in search of more energetically rich finfish species.

Age 1 weakfish diet in Hartman and Brandt's (1995a) study was consistently dominated by pelagic sources (bay anchovy, menhaden). Benthic resources (spot, blue crab, and silver perch) consistently dominated age 1 weakfish diet in littoral habitats. In both studies age 2 fish showed an obvious trend towards increased pelagic prey use in the fall and in May-June benthic prey items dominated diets. By September fish sampled by Hartman and Brandt (1995a) were clearly relying on pelagic prey. Benthic prey dominated the diet of age 2 weakfish in littoral waters until October, when diet was overwhelming composed of the same pelagic species that had consistently been found by Hartman and Brandt (1995a)(anchovy spp., menhaden). No age 3 or > 3 fish were collected by Hartman and Brandt (1995a). Interestingly, age 3 fish showed a decreasing reliance on pelagic prey over time; however, if small weakfish were recategorized as a benthic prey as item this study's diet analysis suggests consistent benthic dependence would be evident across the study period. Diet of age > 3 fish was consistently pelagic in origin and pelagic proportion increased in the fall in accordance with diet of large fish examined by Hartman and Brandt (1995a). A large proportion of the fall diet, however, was weakfish, once again if weakfish were reclassified, as benthic prey trophic dependence would be overwhelmingly benthic in the fall.

Piscivore diets in this study were found to be much more diverse than those found by Hartman and Brandt (1995a). Despite this diversity at the 50% level the percentage of significant dietary overlaps between age classes of species was identical (24%) to that found by Hartman and Brandt (1995a). Pooling age classes and lowering the percent overlap considered significant provided results that resembled that found by Hartman and Brandt (1995a) in that bluefish and weakfish had the highest indices of between species overlap.

Age specific indices provided similar data in that overlap varied seasonally, overlap was generally less from May-August than from September-November, and highest overlap within species occurred at older age classes. Hartman and Brandt (1995a) combined samples from across a two-month period and chose a significance level of 50%. Samples in this study were examined as single events in order to determine if diet overlap was consistent across short-term intervals. A 60% overlap was considered important. Bluefish had the highest within species and between species overlap in Hartman and Brandt's (1995a) study. In this work, striped bass (n=6) had the highest number of within species overlaps. The majority (n=5) of these overlaps occurred in October when a large number and age diversity were sampled. Weakfish (n=2) diets between age classes also overlapped. Within species interactions across species were much more prevalent in the fall. Weakfish and bluefish did not have the highest degree of dietary overlap (Hartman and Brandt, 1995a); instead all piscivores had an equal number of significant between species overlaps (n=4). Striped bass diet overlapped significantly (>60%) with weakfish and bluefish twice and weakfish and bluefish overlapped twice. Also in contrast, no within species overlap was found in bluefish. Significant overlap occurred only twice between the same species and age classes in consecutive samples in the same month (B1 and W3, Sept.).

Results suggest that overlap is highly variable even over the short period and that no more diet overlap is occurring between striped bass and bluefish than is occurring between bluefish and any other piscivores occupying the same habitat. Standard ecological theory dictates that diet overlap is expected to increase with augmentation in prey abundance during summer months (Steele et al. 1995). Prey density peaked in mid-summer (July, Table 2.3) in this study. All three piscivore species were sampled during this period but diet overlap was not markedly augmented.

Empirical work indicates that many fish species forage selectively based upon relative prey size (Juanes and Conover, 1994a; Paradis et al., 1996; Rice et al. 1997; Scharf et al. 1998; Lundvall et al. 1999; Scharf et al. 2000; Scharf et al. 2003), color (Ibrahim and Huntingford, 1989), evasiveness (Vinyard 1980, 1982; Winfield and Townsend, 1988), activity (Luczkovich, 1987; Croy and Hughes, 1991) and/or capture success (Wahl and Stein, 1988; Ellis and Gibson, 1997). Striped bass, bluefish and weakfish, however, are generally considered opportunistic predators whose diets reflect seasonal and/or spatial alterations in prey availability (Bigelow and Shroeder, 1953; Markle and Grant, 1970; Boyton et al., 1981; Juanes et al., 1993; Lucena et al. 2000; Walter et al. 2003). Prey assembly and relative abundance naturally affect predator foraging strategy and prey specific success (Werner and Hall, 1974; Hart and Hamrin, 1988; Hartman and Margraf, 1992; Scharf et al. 2003). Optimal diet theory predicts that predators should forage selectively on prey that maximize their net energy gain (Schoener, 1971; Greene, 1986). Given the prey assemblage available within this study's littoral shallows and the overwhelming biomass of benthic prey (Table 2.2) the much greater dietary proportion of benthic prey in particular crustaceans should not be as surprising as the findings of Hartman and Brandt (1995a) would suggest. Opportunistic behavior and dietary elasticity allowed piscivores to take advantage of seasonal and/or habitat specific opportunities. Optimal foraging theory assumes that predator fitness increases linearly with net energy gain and that natural selection favors those individuals that can maximize energy gain (Pyke 1984). The dietary elasticity evidenced by striped bass, bluefish, and weakfish in this work suggests that these predators maximize their net energy gain and species survival by taking seasonally taking advantage of the most abundant species available in a given habitat.

The early spring data of this study provides an example and emphasizes the need for across season diet analysis in order to reduce potential bias introduced by short-term seasonal prey abundances. Polycheate (nereis) abundance in the water column increased significantly during the annual spring epitoky (May 10th). This reproductive event resulted in increased polycheate encounter rates and vulnerability as the normally inactive benthic form changed to a sexually active pelagic form. A significantly higher polychaete mass was recorded in all piscivores across all ages during the event and a greater mass of larger bluefish and weakfish was recorded at this time than any other suggesting that the event may be taken advantage of annually. To further emphasize the contributions of this soft-bodied prey, measured mass likely underestimated true consumption because softer smaller prey are evacuated at a much higher rate than other prey items (Kionka and Windell, 1981; Swenson and Smith, 1973) and fish were generally left on ice for approximately 16-20 hours after harvest before gut was removed and frozen thus allowing for further digestion of soft bodied prey and further reducing remaining mass in the stomach. Such intense short-term dietary overlap across species, including a recognized pelagic predator like bluefish, suggests that prey abundance (encounter rate) can at times overwhelming influence piscivore diet. In July, large numbers of age-0 silver perch and silverside were sampled in the study site (Table 2.3). Bluefish, age 2-3 weakfish, and age 2 striped bass diets reflected this increased abundance. An augmented importance across all age classes and species, like that which occurred with polychaetes, was not found.

The biological factors that determine prey targeted or predation success in the field are not well studied or understood. Laboratory studies suggest that predator success is the result of a prey's attack and capture avoidance tactics including anti-predator behaviors, use of structural refugia, and relocation due to predator abundance (Heck and Thoman, 1981; Savino and Stein, 1982a, b; Singh-Renton and Moore, 1990; Stein and Magnuson, 1978; Holmes, 1984; Lima et al., 1985; 1986; Gilliam and Fraser, 1987; Juanes et al., 2003; Scharf et al., 2003.) Avoidance and foraging tactics vary by species and can alter with changes in prey assemblage (Juanes et al., 2003). The importance of relative prey body size to capture success is well established (Juanes and Conover, 1994; Paradis et al., 1996; Rice et al., 1997;

Scharf et al., 1998; Lundvall et al., 1999) and can be determined relatively easily under controlled conditions (Scharf et al. 2003). Consumption of a given prey item is the result of its vulnerability and predator preferences. Vulnerability is the product of a prey's susceptibility to attack, its capture success once encountered, and its encounter rate (Greene, 1983, 1986; Baily and Houde, 1989; Latvik and Targett, 1992; Scharf et al., 2003). Susceptibility is strongly influenced by both the predator and prey's inherent morphology and behavioral characteristics (most often taxon specific) developed during ontogeny (Fuiman and Magurran, 1994; Eklov and Persson, 1995). In general, as piscivores grow their diets broaden to include larger prey (Peters, 1983; Persson 1990, Juanes, 1994) this dietary expansion is provided for by ontogenetic increases in mouth gape and swimming speed (Ivlev, 1961; Osenburg and Mittelbach, 1996). Ratio based trophic niche breadths generally do not expand with ontogeny and tend to narrow for largest predators (Scharf et al., 2000). Relative prey abundance, behavioral characteristics, and habitat conditions affect encounter rates. Prey selection is, therefore, not solely influenced by abundance but is the result of many other factors that influence the relative vulnerabilities of different prey types (Greene, 1986). Any factor that reduces a prey's encounter rate or susceptibility decreases its vulnerability.

In this study, fish diet even within the same age class varied seasonally. Seasonal differences in diet are expected and most likely reflect natural cycles in abundance and/or vulnerability. If we assume that piscivores are opportunist and will take advantage of whatever prey is available; vulnerability becomes the deterministic variable. Since prey vulnerability is the product of predator encounter rate generally modeled as being a positive function of prey size and abundance and capture success rate (Pastorok, 1981; Greene, 1983, 1986; Litvak and Leggett, 1992) and encounter rate, the polychaetes during the spring epitoky presented a prey with maximum vulnerability. Such prey behavior may be as important as predator choice in determining diet content especially for invertebrate prey (Singh-Renton and Moore, 1990). Prey will shift habitats to reduce encounter rates or exhibit other behavioral changes when predators are present even at the expense of reducing forage rates (Stein and Magnuson, 1978; Savino and Stein, 1982a, b; Holmes, 1984; Lima et al. 1985; 1986; Gilliam and Fraser, 1987; Scharf et al., 2003). Many investigators (Cooper and Crowder, 1979; Heck and Thoman, 1981; Lascara, 1981; Coen et al., 1981; Crowder and Cooper, 1982; Savino and Stein, 1982a, b; Minnello and Zimmerman, 1983; Orth et al. 1984; Leber, 1985; Wilson et al., 1990; Sogard and Able, 1991) have found that the cover provided by grasses and macro algae can significantly reduce predation. Protection from predation is the primary explanation offered to explain the high densities of prey species and young of the year piscivores in the drift algae and grass bed habitats of littoral zones (Thorhaug and Roessler, 1977; Gore et al., 1981; Thayer and Phillips, 1977). In the Chesapeake, seagrass meadows experience maximum growth and biomass from April to July, massive leaf loss from July to September, and a short-lived secondary growth spurt and biomass increase during the fall and early winter (Orth and Moore, 1986). Reductions in grass blade density and its correlation to habitat complexity infer decreased protection from predation by fishes and birds (Werme, 1981). If prey behavior influences encounter rates and/or relative capture success, then diet data should show a preference (Singh-Renton and Moore 1990). The marsh grasses (Cicchetti, 1998; Currin et al., 1984), and macro algae beds (Nelson, 1979; Coen, 1979; Heck and Thoman, 1981; Sogard and Able, 1991) that dominated the study site; however, also provided increased protection from predation pressures and these flora do not experience the same mid-summer floral defoliation as eelgrass. Prey species that are exposed as eelgrass defoliates likely seek shelter in other local covers in order to minimize predation risk.

Dietary differences across relatively the same time period likely reflect variations due to predator preferences and habitat specific factors. Large alterations in diet composition studies separated by years or decades from the same area at the same time of year may reflect true alterations in the system's ecology. One of the best uses of such contrasting data sets is the generation of hypotheses for experimental explanations of estuarine processes (Coull, 1985) including mechanisms of structural variation in benthic communities and cumulative human impact on natural systems.

Since the 1990's there has been increasing concern over the appearance of emaciated striped bass that often contain skin lesions during the summer months in the Chesapeake Bay (Overton et al. 2003). Some investigators (Hartman and Brandt, 1995d; Griffin and Margraf, 2003), based on the assumption that the bay's production of striped bass is pelagically dependent (Baird and Ulanowitz, 1989; Hartman and Brandt 1995a), propose that increased diet percentages of benthic prey evidenced in recent striped bass diet studies in the bay (Walter, 1999; Walters and Austin, 2003), suggest that preferred pelagic prey is somehow being limited possibly even by increases in the striped bass population (Hartman, 2003). Others have proposed that limitation of suitable prey (Hartman and Brandt, 1995d; Uphoff, 1998; Overton et al., 2000, Griffin, 2001; Uphoff, 2003) may be responsible for reduced striped bass condition witnessed along the Atlantic coast during the past decade (Overton et al., 2000) and may even play an important role in declining summer condition and increased *Mycobacterium* infections (Uphoff, 2003; Hartman and Margraf, 2003). The piscivore diets evidenced in this study are so different than those found in previous investigation that comparisons in percentage of benthic prey in diet in order to investigate long-term changes in the estuary's habitat composition and resulting prey assemblage would be fruitless. This work and others (Hollis, 1952; Lascara, 1981; Harding and Mann, 2001, 2003; Walter and Austin, 2003; Walter et al., 2003; Pruell et al., 2003) may suggests that diets of opportunistic piscivores in the bay are far more elastic and habitat dependent than previous works have claimed and that benthic increases found in recent works may in large part be due sample location. If diets are far more elastic than previously realized then the bay may be able to support larger populations of striped bass without decimating clupeid stocks as Hartman predicts (2003). An alternate hypothesis that cannot be collaborate by previous littoral studies is that striped bass are indeed being limited by pelagic resources and are becoming increasingly dependent upon littoral prey during warmer months in a effort to make up for this limitation. In addition changes in the bay's physical characteristics turbidity, temperature, and/or oxygen content may also influence striped bass distribution seasonally (Coutant and Benson, 1990; Pihl et al., 1991) thus affecting temporal feeding behavior. The Chesapeake bay experiences high water temperatures and increasing areas of low oxygen in late summer causing physiological stress for striped bass (Hartman and Brandt, 1995a) conditions that may result in less effective feeding (Coutant, 1985). Clearly more spatially comprehensive diet analysis and physiological investigations need to be conducted across age classes to determine which factors most influence condition and thus aid in determining whether prey limitation and/or habitat deterioration are to blame. Once limiting parameters are identified the system can better managed to sustain maximum production.

As our knowledge of habitat specific trophic interactions grows it is becoming increasingly apparent that system-wide averages of predator and prey abundance's that do not incorporate effects of spatial variation are likely inadequate for improving understanding of production dynamics or predator and prey interactions (Brandt et al. 1992). Spatial variability in predator and prey interactions is well recognized (Brandt et al., 1992). Dietary comparisons between distinctly different habitats within the bay and other regions suggest that piscivore diets are spatially diverse and are likely related to local prey assemblage structure and vulnerabilities. Habitat specific trophic processes are particularly important to fish production and spatially explicit models of that production. The Magnuson-Stevens Act of 1996 recognizes the importance of spatial variability to production and the scale-dependent linkages between biological function and biological and physical structure in its focussed on identification of Essential Fish Habitat (EFH).

The central premise of the Habitat Suitability Index (HIS) (FWS, 1980a, 1980b, 1981; Terrel and Carpenter, 1997), developed by the U.S. Fish and Wildlife Service as a means of linking fish stocks to habitat, is that the "value" of an area of "habitat" is determined by its carrying capacity as it relates to density-dependent population regulation (FWS 1981). Suitable prey availability may be the overriding factor motivating habitat use by piscivores (Hartman, 2000; Juanes et al., 1993; Lucena et al., 2000; Grecay and Targett, 1996, Hartman and Brandt, 1995a). Optimal forage theory assumes that natural selection favors the development of feeding preferences that maximize energy gain, feeding behavior and habitat choice are thus based on optimizing net energy gain (Enlem, 1966). Establishing piscivore densities within habitats provides a means of comparing biological function between habitats based on species diversity and abundance. Establishing piscivore diet breadth and gut fullness indices in habitats provides a means of comparing potential piscivore carrying capacity between habitats based on diet diversity and energy acquisition. Loss of diet diversity may augment dietary overlap (competition) between piscivores (Setzer et al. 1980; Mercer, 1983) and restrict predator production (Pope, 1979) and prey supply (production) can limit predator production, if availability does not meet demand (Carpenter, 1985; 1987). Piscivores of many different ages consume a wide variety of prey items seasonally in the Chesapeake's littoral zones. The majority of prey consumed relied on the benthic productivity of the littoral zones for their sustenance. Piscivorous consumption, therefore, provided a trophic relay (Knieb, 1997) that directly linked littoral productivity to ocean productivity. Such a direct energetic linkage is likely important to the energy budgets of both environments (Deegan, 1993; Deegan et al., 2000). In addition, to establishing such important ecological linkages, this study strengthens the case for littoral habitat preservation by directly linking the habitats prey diversity and production to that of piscivores. Habitat loss is one of the leading reasons for diminishing species diversity (Minns, 1999) and littoral habitats are the marine habitat that is most often altered by anthropogenic development (Odum, 1971). Such spatially explicit work may have implications for the design of marine reserves in coastal regions (Thorrold et al., 2001).

Fisheries scientist will continue to be faced with an increased demand for management decisions to be based on an ecosystem perspective (Brandt et al., 1992) and spatially explicit ecological models that can forecast system response due to future anthropogenic alterations. Habitat specific spatial processes are particularly important in fisheries' models and will have implications for the design of marine reserves (Thorrold et al., 2001). Future works should continue to expand our knowledge of specific habitat functions as they apply to piscivore production in order to preserve our systems productivity of these valuable fishes. To more fully explore the role littoral habitats play in the production of upper level fishes, future work should establish growth and consumption based on field estimates of daily ration within these zones throughout the period of residence. Bioenergetic models should be applied to determine how energy is apportioned to growth, reproduction, and maintenance. Energy budgets will allow for functional comparisons between subsystems regardless of ecological niche (Healey, 1972). Habitat-specific quantification of contributions to the production of upper level fishes is necessary to the development of spatial modeling efforts and identification of essential fish habitats based on resource acquisition and/or energetic benefits. Management recognizes that the identification and preservation of such habitats is paramount to the future of the fisheries (MSFCMA, 1996).

CHAPTER 4. STRIPED BASS, BLUEFISH, AND WEAKFISH GROWTH ATTAINED IN A MESOHALINE LITTORAL ZONE OF CHESAPEAKE BAY: DEVELOPMENT AND EXPERIMENTAL TEST OF BIOENERGETIC MODELS

ABSTRACT

The Chesapeake Bay's vegetated littoral zones are well documented for their high levels of primary and secondary production. From April to November of 2001 the haul –seine gear was used to surround and collect striped bass, bluefish, and weakfish occupying 144,500 m^2 of Chesapeake Bay littoral zone. Gut content of fishes was subsequently examined and consumption estimates formed. Based on field-derived estimates of nocturnal consumption of mesohaline littoral nekton determined using Eggers model, bluefish and weakfish attained high growth rates from May to November. High water temperatures and insufficient consumption and resulting metabolic stress resulted in weight loss by striped bass. Poor physical condition resulting from physical stress and a lack of energetic inputs may make striped bass more susceptible to disease during this period. Various investigators have suggested that fish can gain temporary metabolic advantages from thermal sanctuaries provided by deepwater. Low daytime littoral densities of piscivores suggest daytime residence in deeper waters or a significant difference in diel gear avoidance. The metabolic consequences of this residence were modeled to quantify effect on each species' growth. Bluefish significantly improved their energy acquisition by occupying daytime thermal sanctuaries. Weakfish benefited but to a much lessor degree. Resident striped bass offset some energetic losses during warm water periods but net positive growth did not result. Growth models were based on

nocturnal littoral ration and estimated consumption. Models predicted that bluefish and weakfish feeding in littoral zones attained better growth rates and improved final mass in comparisons with fishes collected from across Chesapeake Bay habitats. These findings suggest that vegetated littoral zones played a larger trophic role in the production of these two piscivores. Historic reductions in the extent of littoral vegetation, a habitat widely recognized for its production of important piscivore prey, may have limited the Bay's capacity to produce bluefish and weakfish. Striped bass models demonstrated that the effects of temperature on metabolism overwhelmingly influenced their growth during the study period. Findings suggest that resident striped bass endure energetic losses to escape energetic cost and predation risk associated with migration. Compensatory growth in cooler water temperatures of fall and winter may offset the energetic losses these residents experience during summer. Migratory striped bass show substantial growth during the fall period.

INTRODUCTION

It is generally recognized that the elevated primary productivity in some habitats leads to increased levels of secondary production (Odum, 1971). Differences in secondary prey biomass and availability affect predatory fish condition (Grecay, 1991; Lankford and Targett, 1994; Hartman and Brandt, 1995d; Grecay and Targett, 1996b, Lankford and Targett, 1997), which is energetically linked to stock productivity and sustainable harvest level. Habitat specific density–dependent processes may significantly affect production dynamics at the population and ecosystem level (Brandt et al. 1992). If prey availability does not meet predator demand, production at higher trophic levels can be limited (Carpenter et al., 1985, 1987). The Magnuson Stevens Fisheries Conservation and Management Act (MSFCMA) recognizes the importance of identifying and preserving prey producing habitats and identifies this objective as being paramount to the future of the fisheries (MSFCMA 1996).

Knowledge of habitat specific growth dynamics of commercially, recreationally, and ecologically important piscivores such as striped bass, bluefish, and weakfish is increasingly important as fisheries managers attempt to deal with habitat related reductions in productivity and to make decisions based on an interdisciplinary ecosystem perspective. This perspective is a result of the realization that disturbances in part of the system can permeate throughout the food web, thus linking water quality with fisheries production (Carpenter, 1988). Eventually, by combining spatial aspects of habitat-based productivity estimates, environmental forcing functions, and stock assessment data diagnostic models capable of predicting future harvest will result based on the ecological composition and productivity of the whole system. This approach to management is already being tested for pink shrimp (*Penaeus dourarum),* which depend upon the seagrass-mangrove system as a nursery. Fluctuations in the environmental condition of this habitat affect survival, growth, and recruitment. Using a multiple regression analysis, which combines fishery catch statistics and the environmental factors, predictive models have been run that have forecast actual landings within plus or minus 20% for five out of eight years (Sheridan, 1996). Such models may furnish the ecological guidelines for marine communities that, when adhered to, provide for sustainable harvest.

Littoral zones are among the most productive subsystems in estuaries (Odum, 1971). The rich primary productivity of these shallows trophically supports a diverse assemblage of transient finfish, shellfish, and crustaceans. Williams (1973) estimated that eelgrass beds in an estuarine system near Beaufort, North Carolina supplied as much as 64% of the total primary production and that much of this production was exploited by man via commercial fisheries. Vegetated littoral habitats are highly productive with regard to piscivore prey species (Edgar and Shaw, 1995a,b; Howard et al., 1989; Edgar et al., 1994). Small fish assemblages have been found to be twice as abundant in vegetated littoral habitats as in nonvegatated (Edgar and Shaw, 1995a).

Crustacean biomass is positively correlated with that of submerged grasses (Howard et al., 1989; Edgar et al., 1994) consequently seagrass beds contain a high biomass and diversity of benthic and epibenthic species. Littoral investigations show that crustaceans can be trophically important to various age classes of transient fishes (Carr and Adams, 1973; Brook, 1977; Lascara, 1981; Edgar and Shaw, 1995c; Harding and Mann, 2001; Nemerson and Able, 2003). Larger crustaceans, forage fishes, and juvenile piscivores consume small crustaceans; these species are in turn preyed upon by larger adult piscivores (Hartman and Brandt, 1995a; Adams 1976 a, b, Edgar and Shaw, 1995c). Given an increased trophic reliance on crustaceans and shallow water fish prey it is not surprising that littoral fish production has been found to be more reliant on benthic pathways (Lascara, 1981; Edgar and Shaw, 1995b, Nemerson and Able, 2003).

Unfortunately, the littoral zones of the Chesapeake and its adjoining Delmarva Peninsula have experienced substantial habitat alterations (Roman and Nordstrom, 1996; Titus, 1998; Barnard et al., 2001) including a drastic decline in eelgrass coverage (Orth and Moore, 1983, 1984). The effects this habitat loss and its corresponding reductions in prey resource production and refugia have had on the Bay's piscivores are unclear. Loss of refugia may have increased accessibility of both forage species and juvenile piscivores. Severe depletion of either due to predation will potentially result in lower fishery yields (Boesch and Turner, 1984). Littoral habitat alterations may have precipitated a shift in the distribution of prey species (Ruiz et al. 1993) and/or altered forage species assemblage structure. Both

Baird and Ulanowicz (1989) and Hartman and Brandt (1995a) argue that piscivore production is currently mainly reliant on pelagic prey items. In addition, comparisons of field-derived consumption estimates (supply) to potential consumption (demand) suggest striped bass, bluefish, and weakfish production in the bay is currently being limited by prey supply (Hartman and Brandt, 1995d). Large discrepancies in trophic pathway reliance between studies and apparent prey limitation (Hartman and Brandt, 1995d) emphasize the need to further investigate the spatial aspects of trophic interactions. Habitat dependent predator-prey interactions must be identified and quantified (consumption) to improve our understanding of ecosystem mechanics and provide a means of comparison between habitats. Production potential is one of the criteria that can be used to identify essential fish habitat (MSFCMA, 1996). Habitat specific growth models provide a means of assessing comparative value based on production. Once production value is established habitats can be ranked and preserved or restored based upon their production potential. By maximizing potential fish producing habitats a more beneficial environment for fish production can be maintained and future piscivore production provided for.

Simulation modeling is a well-established tool for studying and managing biological systems (Clark, 1985; Walters, 1986). Bioenergetic models are based on species-specific physiological attributes and are capable of predicting consumption from growth or growth from consumption. By applying field data to the Eggers' model (1977) consumption can be determined. Realized growth can be calculated, with the addition of a few needed parameters, to provide a habitat-specific measure of functional value. Analyzing a habitat's value based on its functional contributions to piscivores rather than simple numeric abundance may be a more useful way of examining community organization (Engelmann, 1968). Bioenergetic models can be linked directly to the habitat to examine complex spatial and temporal processes among predator and prey and environmental condition (Bevelhimer, 1990; Brandt et al., 1992). Such spatially explicit models have already been used to compare seasonal habitat suitability (Brandt and Kirsh, 1993), growth potential (Goyke and Brandt, 1993), and predation risk (Mason and Patrick, 1993). Such spatially explicit and temporal models are needed to describe the functional aspects of both the abiotic and biotic marine ecosystem and predict how these processes affect fish production (Bevelhimer, 1990; Brandt et al., 1991, 1992). Determining habitat-specific contributions also provides for direct comparison between habitats regardless of their ecological niche (Healey, 1972), which aids in the identification of essential fish habitats. Basing habitat comparisons on seasonal fish production rather than a few point samples of biomass provided substantial improvement in the assessment of the habitat based on its ability to support production as recommended by Magnuson Stevens (1996).

The seasonal growth dynamics of estuarine piscivores have been little studied (Hartman and Brandt, 1995a). Bioenergetic models temporally reflect changes in feeding, respiration, and growth resulting from modification of metabolism due to alteration in environment, developmental stage, and /or physiological condition (Klekowski, 1970). The physiological parameters necessary to construct bioenergetic models of striped bass, bluefish, and weakfish have been determined in the laboratory by Hartman and Brandt (1995b). Measuring growth and consumption under laboratory conditions, however, may not represent growth and consumption occurring under natural or field conditions (Adams, 1976b). Field based experiments should be undertaken to investigate the relationship between these parameters and food resources because the effects of fish density and food supply on fish production in artificial environments is so strong that it forms the basis for management of the aquaculture industry (Edgar and Shaw, 1995b). This study developed species-specific bioenergetic models based on field derived consumption estimates in a typical partially vegetated Chesapeake Bay littoral zone to determine the habitat's growth contributions to striped bass, bluefish, and weakfish. Models relied upon the temperature and size dependent metabolism equations of Hartman and Brandt (1995a,b). Field consumption estimates determined using the Eggers model (1977) were compared with maximum consumption estimates produced in the laboratory (Hartman and Brandt, 1995b). The models that follow depend upon various laboratory and field research efforts and are the results of this cumulative knowledge and information.

The objectives of this chapter are to: 1) model the growth of adult striped bass, bluefish, and weakfish based on consumption of prey, determined by nocturnal field sampling, in a mesohaline littoral zone, 2) examine the potential energetic benefits of use of surrounding deep waters as temperature refuge by each species, and 3) test various parameters in growth models for sensitivity.

STUDY SITE, SAMPLING PERIODICITY, AND METHODS

Study site, sampling periodicity, and field and laboratory methods

A complete description of the study site, sampling periodicity, and field and laboratory methods can be found in the preceding chapters. Nocturnal diet content discussed in previous chapter provided daily ration estimates. Sampling twice monthly provided ration estimates at less than three or four-week intervals which were needed to provide accurate long-term consumption rates (Trudel and Boisclair, 1993) and provided enough time to reset and mend gear.

Modeling methods

The modeling objectives of this work were accomplished through two related but independent models. A model of maximum daily consumption (C max) that includes fish size and water temperature dependent parameters was constructed to determine each species C/C max ratio. This ratio was used to compare field-determined consumption (Eggers, 1977) to potential maximum consumption based on Hartman and Brandt (1995b) laboratory experiments. The C/C max ratio provides a means of comparing interspecies and intraspecies rations across seasons. The final model was a bioenergetic model that estimated growth based on consumption determined through the Eggers' method (1977). It included various environmental and species-specific metabolic parameters determined by field conditions and Hartman and Brandt's (1995b) piscivores physiology work.

Consumption model

Bioenergetics models of striped bass, bluefish and weakfish can provide accurate estimations of consumption based on growth but have thus far proved less effective at predicting growth from consumption (Hartman, 1993). These failures, however, have been explained in most cases by inaccuracy in field estimates of consumption (Hewett et al., 1991; Ney, 1993). In this study, consumption (C) was determined by applying the approach developed by Bajokov (1935), Eggers (1977) and Elliot and Persson (1978) to field determined stomach content. The Eggers method was preferred due to large within sample variation in stomach content and a lack of consecutive samples required by the approach of Elliot and Persson (1978). The method has been shown to be a good estimator of consumption based on field stomach content (Boisclair and Leggett, 1988) when sampling is not conducted at discrete time intervals. The traditional principal assumption of the approach was that the initial and final levels of food in the stomach over the examined time period were equal (Eggers, 1979; Bosclair and Marchand, 1993; Pennington, 1985). In situ experimental evaluations have shown that this assumption is not essential to the model's application and that the approach can be applied to species that feed throughout the day on a wide range of prey types, that exhibit occasional feeding peaks, or that do not have rigid feeding periodicities (Boisclair and Leggett, 1988).

$$C_{24} = T * S^{\Psi} * E, (1)$$

where

C = consumption in g g^{-1} d^{-1},

T = hours in period of ingestion,

S = mean stomach content (grams prey/ gram predator),

Ψ = a derived constant equal to 1,

and E is the evacuation rate.

The results of diel haul-seine surveys indicate that predators predominantly use littoral zones at night and thus the majority of their trophic intake is also derived at night. The number of hours of darkness can be derived by subtracting the function photoperiod = 11.75 –2.25*cos (2PI*(JD+10)/365) (Wetzel and Neckles, 1986 NEED) from 24 hours. The stomach fullness index (S = sum weight of food category/ sum weight fish examined) (Cortes, 1997; Spraker and Austin, 1997) was assumed to be representative of the average food mass and composition ingested by a typical fish during a given nocturnal period. Ingested prey items were identified to and categorized by species when possible. In some cases minor contributions and/or an inability to identify to species based on remains necessitated that functional groups based on taxa be formed. For a full explanation of taxa based prey groups see the appendix model text section.

Evacuation rates

Evacuation rates were estimated using the Elliot and Persson (1978) model:

$$E = \alpha e^{\beta T,} (2)$$

where alpha and beta are estimated parameters. Alpha is determined by the prey content consumed and beta is a product of the predator's metabolism. A value of .115 is generally accepted as a reasonable estimate of beta for teleost fishes (Durbin et al., 1983) and was applied universally in this study.

Knowledge of gastric evacuation rates in fishes is essential in accurately determining in situ estimates of consumption (Cortes, 1997). Rates are affected by temperature, predator body size, prey type, meal size, and method of feeding (Hurst and Conover, 2001). The degree to which each variable affects a species evacuation of varied prey is unclear. Kionka and Windell (1981) and Swenson and Smith (1973) found that prey size influenced digestion rate more than substance. Weisburg et al. (1981), Juanes and Conover (1994b), and Dos Santos and Jobling (1995) found that evacuation rates of the various diets consumed by the species examined were similar. Until species-specific evacuation rates for the various prey items consumed are conducted, parameters must be estimated based on work done on closely related species and similar prey items (Hansen et al., 1993; Ney, 1993). What is very clear in the literature is that most fish diets vary seasonally in content. These prey items often vary greatly in their digestion rates; therefore, taxa and size specific application of digestion rates may provide more accurate consumption estimates seasonally and annually (Hurst and Conover, 2001).

The feeding mechanisms of striped bass and weakfish differ substantially from bluefish. Striped bass and weakfish ingest prey species whole, naturally sizes of consumed prey vary greatly. Evacuation rate has been found to be affected by prey size (Smith et al., 1989; Andersen, 1998) and content (Lankford and Targett, 1997). The evacuation rates of spot and blue crab vary significantly (Van Montfrans, personal communication) in striped bass, as do the digestion rates of mysid shrimp and *Crangon* prey in juvenile weakfish (Lankford and Targett, 1997). Bluefish, unlike striped bass or weakfish, are equipped with very sharp teeth a physiological advantage that allows them to take bite size pieces of prey. This morphological difference enables them to consume much larger prey than their mouth gape would allow them to swallow. This alternative method may provide them with a larger range of prey species and/or diet (Scharf et al., 1998). In addition, reducing ingested prey to bite size portions decreases digestion time thus increasing evacuation rates. This ingestion approach may in part explain the uniform digestion rates found in bluefish examined by Juanes and Conover (1994b).

Unfortunately, the gastric evacuation rates of all prey taxon from striped bass, bluefish, and weakfish have not been determined. A lack of species-specific data necessitated that digestion rates be based on those of other teleosts; this is an accepted approach when species-specific data do not exist (Hansen et al., 1993; Ney, 1993). Large bodied shrimp have been found to be digested slower than smaller shrimp or soft-bodied prey (Nelson and Ross, 1995; Singh-Renton and Bromley, 1996; Lankford and Targett, 1997). Unfortunately, no blue crab specific rates have been established. Lankford and Targett (1997) found that small crustaceans (*mysid*) were evacuated from weakfish stomachs 1.8 times faster than medium hard-shelled crustaceans (*Crangon*). Based on this finding and a similar size increase between blue crab and *Crangon,* a blue crab digestion rate was estimated by dividing Lankford and Targett (1997) rate of medium crustacean evacuation .008 by 1.8. The estimate of .0044 seems appropriate because it matches the slowest digestion rate found in the literature; a rate determined for Atlantic cod and large food items (.004). This rate has been applied in several studies to estimate the digestion rate of less digestible larger items (Durbin et al., 1983; Overholtz et al., 2000; Link et al., 2002). Table 4.1 summarizes the digestion input data for evacuation rates.

Table 4.1: Size specific digestion rates for prey item categories

Prey group	Alpha	Citation
large fish	.00406	Durbin et al., 1983
small fish	.016	Hartman, 2000
large crustaceans	.0044	Lankfort and Targett, 1997
medium crustaceans	.008	Lankfort and Targett, 1997
small crustaceans	.014	Lankfort and Targett, 1997
polycheates	.04	Bagge, 1977
unknown item	.008	Lankfort and Targett, 1997

The average menhaden and weakfish ingested by weakfish were much larger than other fish species ingested. Due to this large relative prey size a large fish evacuation rate was applied to the weakfish model for these two prey items. A large fish evacuation group appears in the fall striped bass model but it only includes gizzard shad. Though these shad were large so too were the striped bass that consumed them, therefore a small fish evacuation rate was applied to this group. Gizzard shad is considered separately in the fall striped bass model to allow for prey-specific sensitivity analysis. In accordance with the findings of Juanes and Conover (1994b) and Scharf et al. (1998), differences in digestion rates based on fish prey size were not included in bluefish model; differences in digestive rates for crustaceans were. The small fish evacuation rate was applied to the anchovy, benthic fish, pipefish, unknown fish, and all species-specific small fish functional groups. Amphipods, isopods, mysid, and unidentified small shrimp were all categorized as small crustaceans. The medium crustacean evacuation group contained only shrimp and included unknown peneid, crangon, and paleamonetes species. Blue crabs, mud crabs, and mantis shrimp were considered large crustaceans. An evacuation rate of .04 was chosen for polycheates. This is the fastest evacuation rate reported in the literature and was calculated based on the evacuation rate of shrimp tails from Atlantic cod (Bagge, 1977). Realistically, the true evacuation rate of polycheates may be much higher but no published rate for soft-bodied annelids could be found. Unknown items were not found often and generally were composed of hard parts, usually crustacean, that could not be positively identified. This functional group made up such a small percentage of diet composition that contributions were likely insignificant. They were assigned the evacuation rate of .008, the same rate Lankford and Targett (1997) found for medium crustaceans.

If stress occurred during sampling it would depress evacuation rates (Mann, 1967; Swenson and Smith, 1973; Thorpe, 1977; Windell, 1978). Use of active gear as a sampling method (seine) has been found to cause stress and depress evacuation rates as indicated by comparisons with laboratory determined evacuation rates of similar prey items and temperatures (Boisclair and Leggett, 1988). Consequently, some have chosen to make corrections that increase rates so that they match laboratory rates at a given temperature (Boisclair and Leggett, 1988). A second source of potential bias is extended retention time, which prohibits ration intake but allows for continued evacuation (Eggers, 1977). No attempt to correct for depressed digestion or retention time was made in this study, but these findings suggest that true piscivore consumption may be underestimated.

Consumption maximum model

Consumption maximums (C max) for each species were determined at specific age classes expressed as standard weights (this aspect of the equation will be covered in the standardized sizes portion of the text that follows) experimentally by Hartman and Brandt (1995b). The equation that follows includes these experimentally determined functions and is:

$$C\ max = CA * W^{CB} * f(T), \quad (3)$$

where

CA = intercept: C max at ($theta_2$+$theta_3$),

W = standard fish weight,

CB = coefficient: C max vs. weight.

The Thornton and Lessem (1978) algorithm provided the temperature dependency model f (T). For a full description of approach see Thorton and Lessem (1978) and Hartman and Brandt (1995b). The Thornton and Lessem (1978) algorithm is also described in the appendix, section 1 get rid of appendix. For a more detailed description of application of Thornton and Lessem approach and its advantages over Q_{10} approach used by Kitchell et al. (1977) see Hewett and Johnson (1992).

Bioenergetic growth model

Bioenergetic models rely on the balanced energy equation of Winberg (1956):

$$G = C - (R + SDA) - F - U, \quad (4)$$

where

G = growth (somatic and gonadal),

C = consumption,

R = respiration rate,

SDA = specific dynamic action,

F = egestion rate,

and U = excretion rate.

It was assumed in this model as others investigators have in the past (Hartman and Brandt 1995b; Kitchell et al., 1974, 1977; Rice et al., 1983) that egestion (F) and excretion (U) and SDA were constant portions of ingested or assimilated energy. Egestion (F) was modeled as .104 of C and excretion (U) and SDA were modeled as .068 and .172 of assimilated energy (C-F) respectively.

$$R\ (g\ O_2\ g^{-1}d^{-1}) = RA*W^{RB}*e^{RQT}*ACT,\ (5)$$

RA is the intercept ($g\ O_2\ g^{-}1d^{-1}$) for one gm of fish at 0 degrees C, RB is the exponent of the weight – dependence function, W is the wet weight of the fish,
RQ is the temperature dependence exponent and T is the temperature (Hartman and Brandt, 1995b).

R is reported in the units of $g\ O_2\ g^{-1}\ d^{-1}$ by Hartman and Brandt (1995b) and had to be converted to grams wet weight per gram predator per day to match model units. Conversion was computed by inverting the seasonal cal gm^{-1} wet weight of each predator determined by Hartman (1993) and multiplying it by suitable conversion factors: * (3280 cal /gm O2) * (gm O2 $g^{-1}\ d^{-1}/1$) = gm wet weight $g^{-1}\ d^{-1}$.

Energy densities of piscivores (cal gm^{-1} wet weight) change seasonally (Appendix 16) and changes in predator energy content directly affect the cost of respiration. Age dependent density estimates are available in Hartman (1993) and were incorporated into the model because they have direct bearing on the seasonal cost of respiration. See Appendix 17 model assumptions section for details. Seasonal variation in prey energy densities are not incorporated because these data are very scant in the literature and previous error and sensitivity analysis have shown that bioenergetic models are relatively insensitive to these energy density variables (Rice et al., 1983; Stewart et al., 1983; Bartell et al., 1986).

Metabolism is often modeled as R times an activity multiplier (ACT). The ACT component in the respiration model adjusts resting metabolism to active metabolism produced during normal activity such as feeding, swimming, and diel migrations (Winberg 1956, Brett and Groves 1979). The ACT chosen for this model was the mean ACT determined by Hartman and Brandt (1995b). The mean ACT was determined through repeated laboratory observations of measures of growth, consumption, temperature, and energy densities of predator and prey and repetitive solving for ACT so that predicted growth matched observed growth in bioenergetic models. Species-specific ACT parameters and other model inputs can be found in Tables 4.2-4.4.

In nature a portion of the energy allocated to growth in this model will be appropriated to reproductive effort and that a portion of this energy will not benefit the species but will be lost. Due to the species-specific nature of this variable, seasonal and physiological variability, and lack of information on its energetic requirements this energetic loss was not modeled. In addition, modeled mass (W) was based on an average individual and was not intended to address population scale factors such as losses due to predation, fishing, or cannibalism.

ACT alterations

Table 4.2: Symbols and estimated parameters used in bioenergetics models for striped bass. Fall inputs due to variation in catch composition size are indicated.

Parameter Description		Parameter Value	Source
		Consumption C_{max}	
CA	intercept: C max at $(\tau_2+\tau_3)$,	.3021± .1081	Hartman and Brandt, 1995b
CB	coefficient: C max verses weight	-.2523±.082	Hartman and Brandt, 1995b
τ_1	Temperature at K_1 (ave. age 1-2, age 2-3≤ fall)	6.6, 7	Hartman and Brandt, 1995b
τ_2	Temperature at K_2 (ave. age 1-2, age 2-3≤ fall)	18.5, 16.5	Hartman and Brandt, 1995b
τ_3	Temperature at K_3 (ave. age 1-2,age 2-3≤ fall)	28.5, 28.5	Hartman and Brandt, 1995b
τ_4	Temperature at K_4 (ave. age 1-2, age 2-3≤ fall)	31, 31	Hartman and Brandt, 1995b
K_1	Proportion Cmax at τ_1 (ave. age 1-2,age 2-3≤ fall)	.2585, .289	Hartman and Brandt, 1995b
K_2, K_3	Proportion Cmax at $\tau_{2\text{ AND }3}$	.98	Hartman and Brandt, 1995b
K_4	Proportion Cmax at τ_4 (ave. age 1-2,age 2-3≤ fall)	.875, .875	Hartman and Brandt, 1995b
		Consumption	
α	prey dependent	*variable*	See table 4.1
B	constant	.115	Durbin et al., 1983
		Egestion	
F	proportion consumed food egested	.104	Rice et al., 1983
		Excretion	
U	proportion assimilated food excreted	.068	Rice et al., 1983
		Respiration	
RA	Intercept: R (g O_2 d^{-1})	.00028 ± .0005	Hartman and Brandt, 1995b
RB	Coefficient: R verses weight	-.218 ±.0005	Hartman and Brandt, 1995b
RQ	Coefficient: R verses temp.	.076 ± .0054	Hartman and Brandt, 1995b
S	Coefficient: specific dynamic action (proportion assimilated food)	.172	Hewett and Johnson, 1992
ACT	Coefficient: multiplier of metabolism	1.649 ± .206	Hartman and Brandt, 1995b

Table 4.3: Symbols and estimated parameters used in bioenergetics model for age 0 through 2 bluefish.

Parameter Description		Parameter Value	Source
		Consumption C_{max}	
CA	intercept: C max at (τ_2+τ_3),	.5197 ± .2907	Hartman and Brandt, 1995b
CB	coefficient: C max verses weight	-.0288 ±.0142	Hartman and Brandt, 1995b
τ_1	Temperature at K_1	10.2	Hartman and Brandt, 1995b
τ_2	Temperature at K_2	23	Hartman and Brandt, 1995b
τ_3	Temperature at K_3	28	Hartman and Brandt, 1995b
τ_4	Temperature at K_4	32	Hartman and Brandt, 1995b
K_1	Proportion Cmax at τ_1	.156	Hartman and Brandt, 1995b
K_2, K_3	Proportion Cmax at $\tau_{2\ AND\ 3}$	.98	Hartman and Brandt, 1995b
K_4	Proportion Cmax at τ_4	.85	Hartman and Brandt, 1995b
		Consumption	
α	prey dependent	variable	see table 4.1
B	constant	.115	Durbin et al., 1983
		Egestion	
F	proportion consumed food egested	.104	Rice et al., 1983
		Excretion	
U	proportion assimilated food excreted	.068	Rice et al., 1983
		Respiration	
RA	Intercept: R (g O_2 d^{-1})	.00558 ± .00068	Hartman and Brandt, 1995b
RB	Coefficient: R verses weight	-.264 ± .126	Hartman and Brandt, 1995b
RQ	Coefficient: R verses temp.	.06925 ± .0160	Hartman and Brandt, 1995b
S	Coefficient: specific dynamic action (proportion assimilated food)	.172	Hewett and Johnson, 1992
ACT	Coefficient: multiplier of metabolism	1.8805 ± .328	Hartman and Brandt, 1995b

Table 4.4: Symbols and estimated parameters used in bioenergetics model for age ≥ 1 weakfish.

Parameter	Description	Parameter Value	Source
		Consumption C_{max}	
CA	intercept: C max at $(\tau_2+\tau_3)$	.492 ± .03	Hartman and Brandt, 1995b
CB	coefficient: C max verses weight	-.268±.014	Hartman and Brandt, 1995b
τ_1	Temperature at K_1	14.8	Hartman and Brandt, 1995b
τ_2	Temperature at K_2	25	Hartman and Brandt, 1995b
τ_3	Temperature at K_3	25	Hartman and Brandt, 1995b
τ_4	Temperature at K_4	29	Hartman and Brandt, 1995b
K_1	Proportion Cmax at τ_1	.195	Hartman and Brandt, 1995b
K_2, K_3	Proportion Cmax at $\tau_{2 \text{ AND } 3}$	.98	Hartman and Brandt, 1995b
K_4	Proportion Cmax at τ_4	.97	Hartman and Brandt, 1995b
		Consumption C_k and Sum C	
α	prey dependent	*variable*	*sees table 4. 1*
B	constant	.115	Durbin et al., 1983
		Egestion	
F	proportion consumed food egested	.104	Rice et al., 1983
		Excretion	
U	proportion assimilated food excreted	.068	Rice et al., 1983
		Respiration	
RA	Intercept: R (g O_2 d^{-1})	.002981 ± .0005	Hartman and Brandt, 1995b
RB	Coefficient: R verses weight	-.155 ± .0240	Hartman and Brandt, 1995b
RQ	Coefficient: R verses temp.	.0508 ± .0025	Hartman and Brandt, 1995b
S	Coefficient: specific dynamic action (proportion of assimilated food)	.172	Hewett and Johnson, 1992
ACT	Coefficient: multiplier of metabolism	2.465 ± .721	Hartman and Brandt, 1995b

The ACT variable in the respiration model adjusts resting metabolism to active metabolism produced during normal activity such as feeding, swimming and diel migrations (Winberg, 1956; Brett and Groves, 1979). This value is usually between 1 and 2 based on the relative activity believed to be experienced by the fish (Kitchell et al., 1977; Rice et al., 1983; Hewett and Johnson, 1992). Precision may be particularly uncertain for ACT because it is often an arbitrary value based on the perception of fish activity (Ney, 1990). Hartman and Brandt (1995c) applied a standard ACT to each species throughout their model period. The ACT chosen was that required to balance the energy equation using data from their consumption experiments. Deduced ACT values were similar to those reported for field populations of yellow perch (Boisclair and Leggett, 1989), young walleye (Madon and Cuver, 1993), and young brook char (Boisclair and Sirios, 1993) and the values of 2-3 suggested for active metabolism by Brett and Groves (1979). Examination has shown a positive linear relationship between ACT and specific consumption rate also referred to as daily ration (g /g/day) (Hartman and Brandt, 1995b). This simply implies that ACT is high when the fish are actively searching for food and lower when at rest. Bluefish and weakfish generally consumed a large portion of their maximum daily ration during nocturnal feeding forays into littoral zones and daytime piscivores samples were too small and sparse seasonally to accurately estimate average daylight piscivore ration temporally. Based on field observations and Hartman and Brandt (1995b) maximum consumption estimates, daylight littoral consumption was assumed to be negligible (0) and ACT during daylight hours was set at of 1.

Standardized sizes and ages applied to C max and routine metabolism

Hartman and Brandt (1995b) used field-observed size-at-age ranges as the basis for partitioning standardized sizes and applied these standardized sizes to the consumption maximum (C max) and metabolism equations. Consumption maximum (C max) and routine metabolism equations for each species were determined in the laboratory by Hartman and Brandt (1995b) as temperature and size dependent functions. Standardized sizes based on age as applied by Hartman Brandt (1995b) provided age-based comparisons across species. Standardized sizes were replicated in this work to provide for growth comparisons between species and with their study.

The 1000gm standard size was applied to all models in this study because it best characterized piscivore size range provided by field samples across species. Hartman and Brandt (1995b) selected the 1000 gm standard size class to characterize adult specific growth rates for all three piscivores, therefore, it should provide a robust characterization of adult age classes across species and provide for meaningful comparisons between species in this study. Other standardized sizes did not contain as wide a range of applicable sizes and/or did not include all sampled sizes. For more information on standard sizes and age criteria see Hartman and Brandt, (1995b).

Weakfish over 1000gm were collected in the site in early May and again in late September, presumably while immigrating and emigrating respectively. Low sample size and associated stomach content variability did not provide data adequate to model. Weakfish over 1000gm were omitted from model in order to improve estimation of daily ration and thus growth.

Ontenogenic differences do not affect the C max or respiration equations of adult weakfish or bluefish, therefore, estimating age class of these species is not necessary to improve growth models. Striped bass show larger variation in C max and respiration due to ontenogenic changes and the Chesapeake's population varies in age class distribution and relative abundance seasonally. Most sub-adult striped bass remain in their natal nursery estuary for approximately two years before taking part in coastal migrations (Mansueti, 1961; Massmann and Pacheco, 1961; Setzler-Hamilton and Hallet, 1991). The Chesapeake's population can be partitioned into resident and migratory fish (Chapman, 1987). Based on work by Coutant (1987), the Atlantic States Marine Fisheries Commission (ASMFC) considers and manages fish >711mm as migratory. Fish of this size occurred too infrequently in the spring to be included in spring model. Based on exclusion of migratory fish, life history, estimated age distribution of samples based on size composition, an even distribution of age 1 and 2 fish was assumed during the spring and an average between these age classes' parameters applied to the C max equation.

In the fall, catches of smaller fish were not consistent enough throughout the sampling period to be included in the model. In order to model the new catch distribution, fish < 405gm were excluded from the model. This mass marks the low end of the range (405-2886) used for the 1000 gm standardized size for striped bass routine metabolism (Hartman and Brandt, 1995b). The assumed age applied to C max was increased to include age 3≤ fish. The chosen parameter value was an average of age 2 and 3≤ fish.

Temperatures applied to consumption and C max

Large-scale collection methods required more time for operation and exposed fishes to higher water temperatures than they would normally experience if allowed to migrate to deeper waters as sample abundances suggest. This exposed gut content to daytime littoral temperatures and, therefore, the average temperature over the 24-hour period was applied to consumption and consumption maximum computations.

Validation

Model predictions were validated by comparisons with field-determined growth (Hartman and Brandt, 1995a, Bonzek et al. unpublished) and/or alterations in seasonal energy densities of flesh from fish collected randomly from various Northern Chesapeake Bay habitats (Hartman, 1993).

Effects of diel temperature refuge on growth

Under natural conditions, fishes make habitat selection based on food availability, temperature, and other factors (Ware, 1982; Crowder and Magnuson, 1983). By incorporating these factors into bioenergetic models these factors can be integrated into one model and cost benefit analysis of varied approaches examined (Kitchell et al., 1977; Stewart et al., 1981, 1983). If diel migration to cooler waters deeper waters occurred during daylight hours than surrounding water temperatures would affect fish metabolism. The energetic effects of diel migration and associated temperature variation on growth were examined species-specifically by incorporating habitat specific temperature regimes into temperature dependent respiration equations. Diel migration was assumed normally during model operation. Temperatures used to compute daytime respiration at depth were attained from a remote sensors buoy WE4.2's bottom data (Chesapeakebay.net). This buoy was located a short distance north of the study site in the mouth of the York River in about 10 meters of water. The river channel is much deeper than this buoy and would likely provide greater thermal refuge. Littoral temperatures were acquired by the National Estuarine Research Reserves remote sensing equipment on site by forcing each species to remain in littoral temperatures for the entire 24-hour period the energetic savings of each species migration could be estimated and compared.

Sensitivity analysis

Parameter uncertainty is an area of considerable concern in the application of bioenergetics models (Hansen et al., 1993). Sensitivity analyses of models used to predict growth have been found to be sensitive to as many as seven model specific parameters (Bartell et al., 1986; Beauchamp et al., 1989). Monte Carlo simulation has been used to rank these in order of importance and found that the realized fraction of C max (C-to-C max ratio), the allometric parameters for consumption (α, B), and respiration are of primary importance (Bartell et al., 1986).

Maximum consumption has two allometric parameters for which Hartman and Brandt (1995b) determined 95% confidence intervals CA and CB. The fraction of C max achieved was determined by entering known daily feeding rations into the Eggers (1977) consumption equation and dividing by C max as estimated by Hartman and Brandt (1995b). The C-to-C max ratio was used to determine how much of the maximum daily consumption was being attained during nocturnal feeding forays. It also provided a standard for comparing the habitat's trophic contributions across seasons and species. The daily ration from which growth is derived in the model is not based on a theoretical ration but is instead derived from real field data; therefore, the sensitivities of the model to ratio alterations will not be performed.

Consumption or daily ration directly affects growth. Beta in the consumption formula of Eggars (1977) represents the digestive capabilities of the predator ($E = \alpha e^{BT}$). Based on laboratory analysis teleosts have been determined to be very similar with respect to this characteristic (Durbin et al., 1983). The alpha value in the evacuation term is determined by the digestive characteristics of the prey, a parameter known to be highly variable. An often-applied method of testing a model's sensitivity to a given parameter is to increase or decrease that input by a constant fraction while other parameters remain fixed. Relative changes in model output (annual growth) are then used to assess sensitivities (Kitchell et al., 1977). Species-specific data exist for this parameter and can be used to group prey items based on size and/or taxon. Sensitivity analyses were performed on the various prey groups by altering inputs by 10% as described above to determine effect on predator growth.

Another method of examining a parameter's sensitivity is to increase or decrease the input by the deviations that define a given confidence interval. Respiration has two allometric parameters, which were derived under laboratory conditions and thus contain known confidence intervals. Respiration energetics directly affected fish growth possibly preventing positive growth in the case of striped bass. To test the sensitivities of the models to alterations in respiration each terms 95% confidence interval was added or subtracted.

RESULTS

C/C max and growth model

Striped bass

Two striped bass models were constructed because catch size distribution varied greatly between spring and fall (Appendix 6). Average fish size declined throughout the spring study period and no coastal migrants, based on a size class determined by Coutant (1987) (>711mm), were present. Striped bass disappeared from the littoral zone by late summer. Coastal migrants were present in late fall and average fish size increased throughout the period. Differences in seasonal catch size distribution resulted in varied criteria for model inclusion.

Spring model

The spring model based on fish < 711 mm ran from Julian day 129-205(May 10- July 25). The C-to-C max ratio (consumption ratio) for striped bass in the spring model was consistently lower than either other piscivore (Fig .4.3), never exceeding .42. In the cool waters of early spring consumption was sufficient to result in short term positive growth. C/C max declined until it reached a minimum on Julian day

Figure 4.3- 4.5: Figure 4.3 through 4.5 were generated by the spring striped bass model. Figure 4.3 displays the C/Cmax ratio, which is unitless. Figure 4.4 illustrates energetic losses due to respiration, specific dynamic action (SDA), egestion (F), and excretion (U). Figure 4.5 shows predicted growth during period. All parameters in 4.4 and 4.5 are in units of gm wet weight.

Fig. 4.3

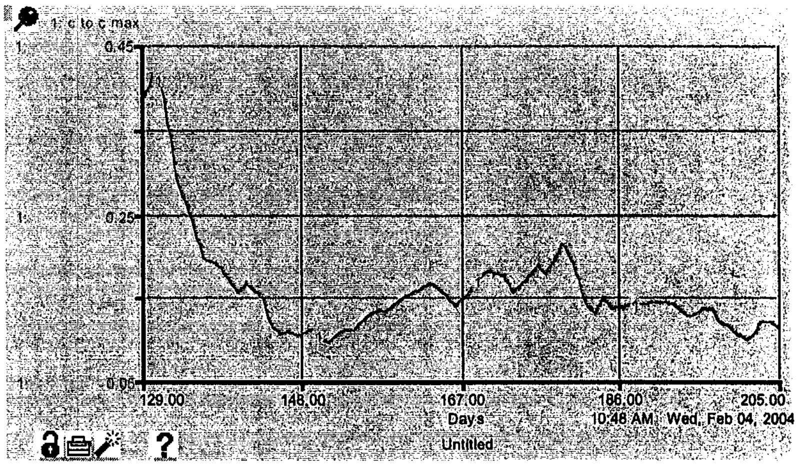


Fig. 4.4

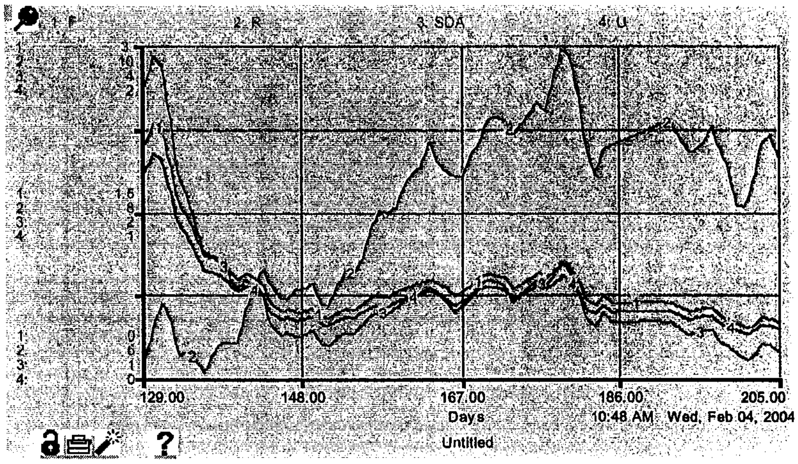
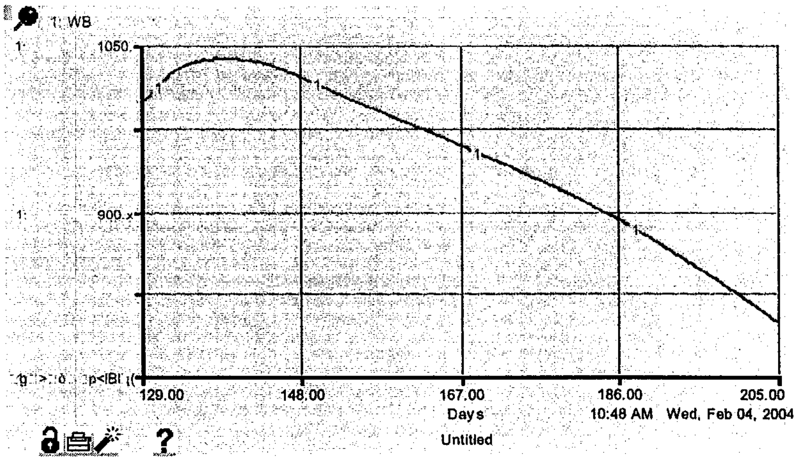


Fig. 4.5



150 (May 31). As water temperatures continued to rise, average fish size decreased presumably because larger fish moved offshore and dietary diversity was augmented. C/C max recovered concurrently with diet diversity augmentation but recovery was not sufficient to offset increasing respiratory cost (Fig 4.4). Mass and presumably overall physiological condition declined due to warm water temperatures stresses (Hartman and Brandt, 1995b) were not offset by trophic energy acquisition. By July the model predicted that fish would lose 20% of their original mass (1000gm May 10 to 797gm by July 25, Fig. 4.5).

Fall model

The fall model ran from Julian day 267 (September 25) until the study's end on 322 (November 19) and was based on fish 405gm ≤. The C/C max ratio in early fall started off very low (.11) a percentage that was even lower than that recorded in late spring (Fig. 4.6). Poor consumption and over burdensome temperatures lead to initial declines in growth. As littoral water temperature declined in October a large immigration of striped bass into the site occurred (Tabel 2.5). C/C max was augmented as larger immigrants preyed upon abundant gizzard shad (Fig. 4.7). Concurrent increases in consumption and water temperature declines resulted in net positive growth for larger fish during the lat fall (Fig. 4.8).

Bluefish

Figure 4.6- 4.8: Figure 4.6 through 4.8 were generated by the fall striped bass model. Figure 4.6 displays the C/Cmax ratiowhich is unitless. Figure 4.7 illustrates energetic losses due to respiration, specific dynamic action (SDA), egestion (F), and excretion (U). Figure 4.8 shows predicted growth during period. All parameters in 4.6 and 4.7 are in units of gm wet weight.

Fig. 4.6

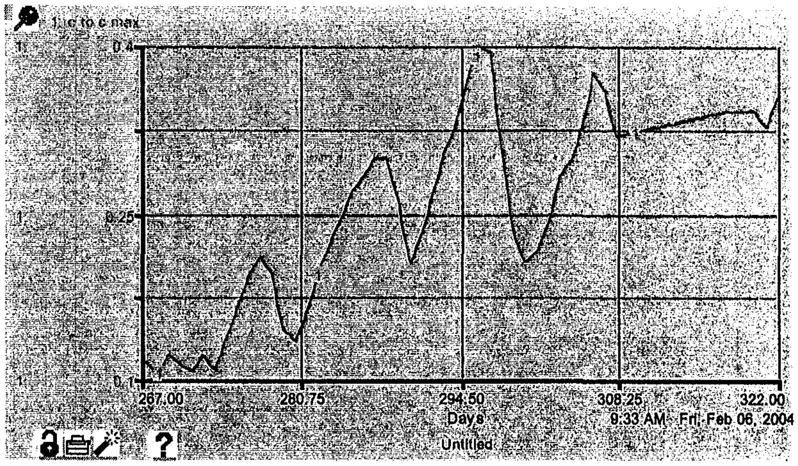


Fig. 4.7

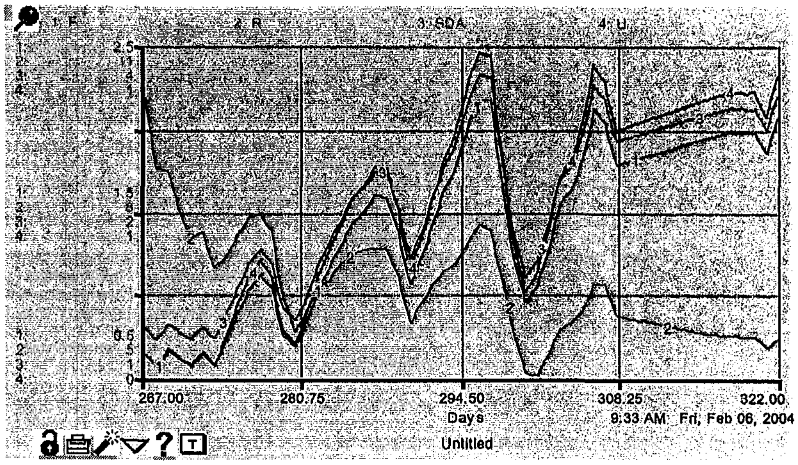
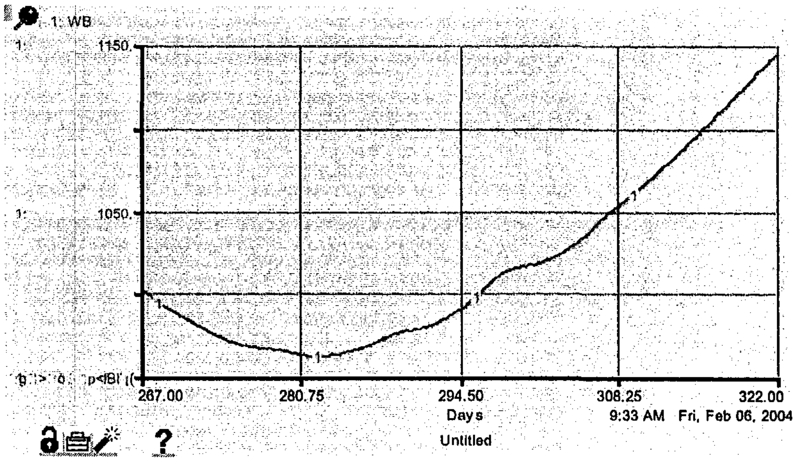


Fig. 4.8



The bluefish model ran from the start of the study period Julian day 129 (early May) until day 322 (late November). C-to-C max ratio had an enormous range from .09 to .96. It was low (.16) in the spring and fall (.30) and highest in conjunction with peak water temperatures in late summer (Fig. 4.9). Bluefish achieved good growth from the resources they foraged out of the littoral habitats. A fish entering the area in May at 400gm could reach 1409gm by late September (Fig. 4.10). The model predicts that fish that remained in the study area after late September, of which there were very few, would experience weight loss and leave the zone in mid-November weighing 1241gm. Lower fall C-to-C max ratios may be due to competition from large schools of immigrating striped bass or severely reduced sample sizes. The 5 fish captured in October and 3 in November likely provided inadequate sample sizes necessary to define daily ration. Respiration costs increased proportionally in the cooler waters of fall as they had in spring (Fig. 4.11).

Weakfish

The weakfish model also ran for the entire study period. Weakfish consistently had the highest average C-to-C max ratio, but the ratio varied greatly from .08 to over 1. The ratio actually surpassed 1 on three occasions, once in early summer and twice in the fall (Fig. 4.12). Theoretically C max should not be surpassed however, it must be remembered that C max was estimated based on laboratory (Hartman and Brandt, 1995b) consumptions of regimented bay anchovy and menhaden diets. A theoretical C max was then calculated based on fitting a

Figure 4.9- 4.11: Figure 4.9 through 4.11 were generated by the bluefish model. Figure 4.9 displays the C/Cmax ratio, which is unitless. Figure 4.10 gives energetic losses due to respiration (R), specific dynamic action (SDA), egestion (F), and excretion (U). Figure 4.11 shows predicted growth during period. All parameters in 4.10 and 4.11 are in units of gm wet weight.

Fig. 4.9

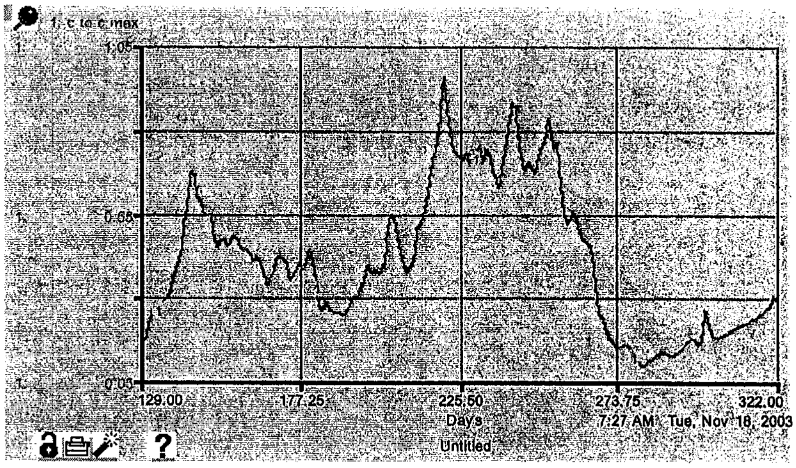


Fig. 4.10

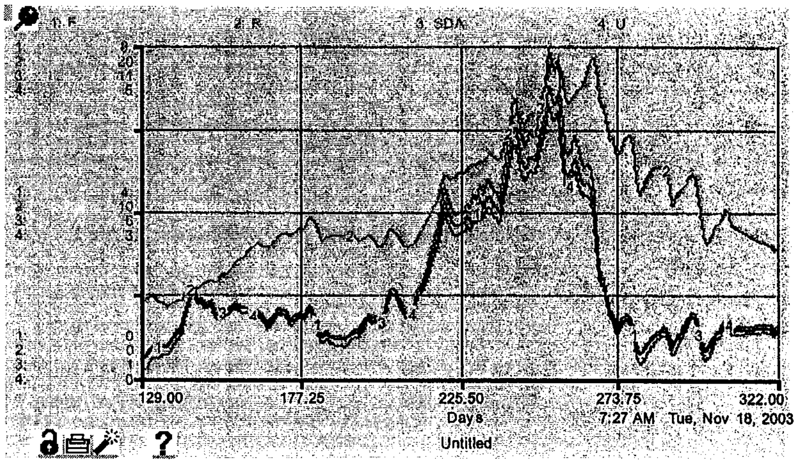


Fig. 4.11

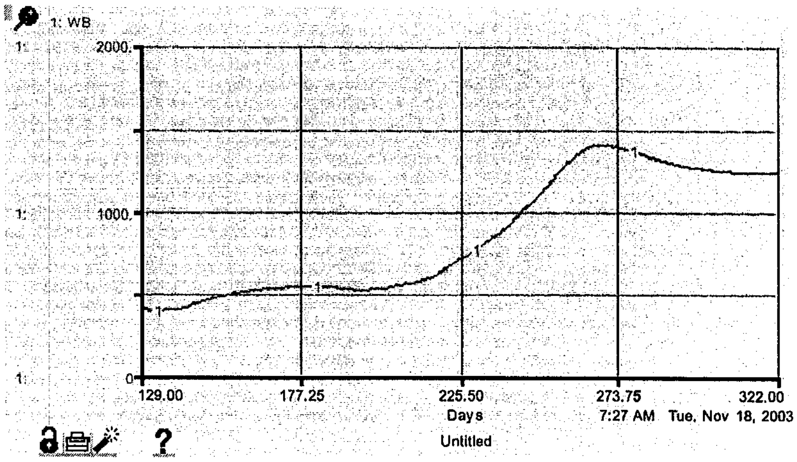


Figure 4.12- 4.14: Figure 4.12 through 4.14 were generated by the weakfish model. Figure 4.12 displays the C/Cmax ratio, which is unitless. All parameters in 4.13 and 4.14 are in units of gm wet weight. Figure 4.13 illustrates energetic losses due to respiration, specific dynamic action (SDA), egestion (F), and excretion (U). Figure 4.14 provides predicted growth during period.

Fig. 4.12

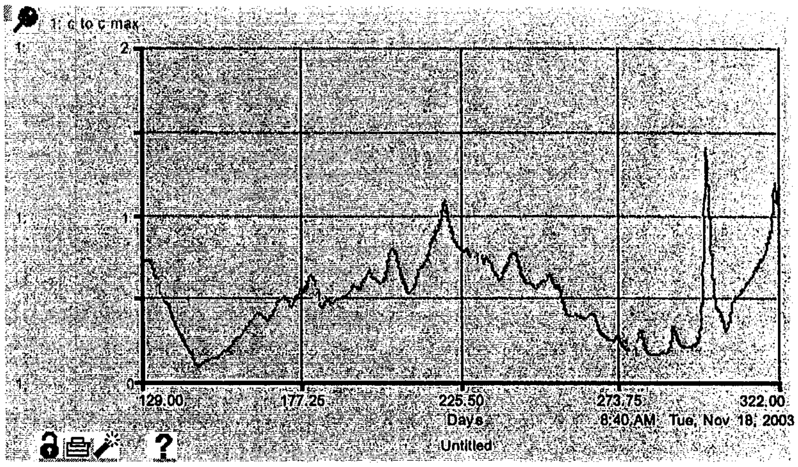


Fig. 4.13

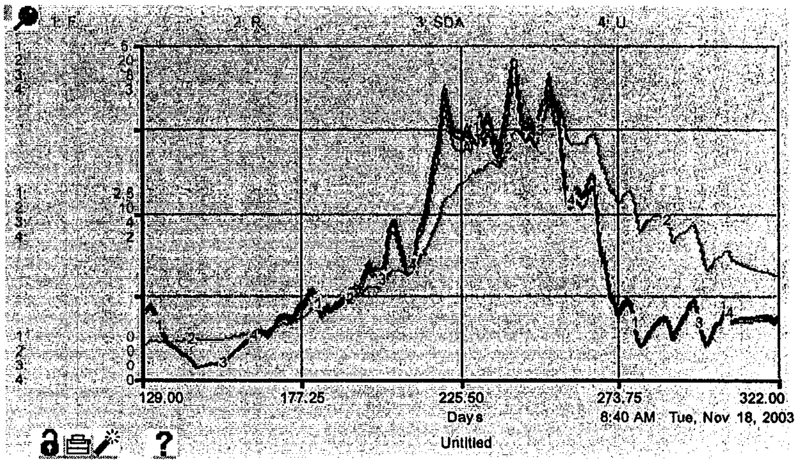
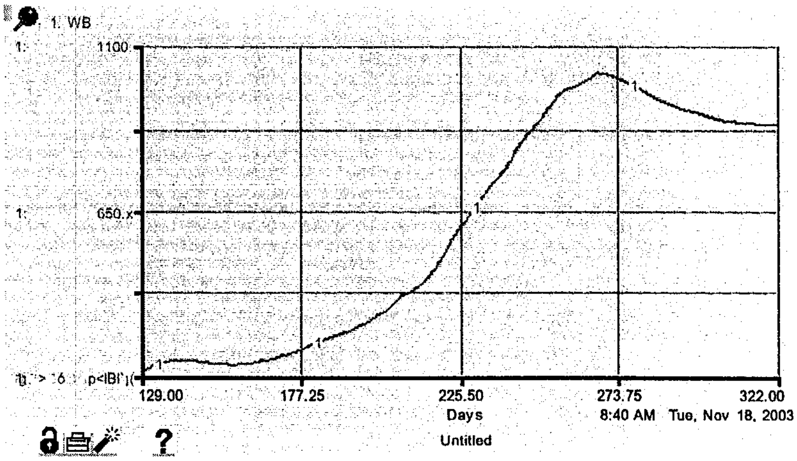


Fig. 4.14



regression to average maximum consumption across fish sizes. Predicted C max, therefore, is based on a mean consumption determined in the laboratory based on feedings of small proportions to conditioned laboratory fish. Greater ingestion rates in the field may reflect availability of larger prey items and/or different predation responses due to captivity.

Weakfish achieved well above 50% of C max during nocturnal feeding forays from late June through September. Exceptional growth resulted with the average 211gm fish in May growing to 1025gm in September (Fig. 4.13). Similar to the findings in the bluefish model, late September is the optimal time to depart the shallows of the study site. Fish that remained experienced a loss in condition and a final mass of 889gm by November. Loss in condition in the fall resembled that predicted for bluefish. Reductions in consumption may have been due to increased competition with or predation risk from increasingly abundant striped bass. Losses may also be an artifact of smaller sample sizes. In addition, respiratory cost was proportionally greatest in the fall (Fig. 4.14)

Validation

Field determined age-specific striped bass growth results during the spring model period (Julian day 129-205) show different growth rates for age 1 and 2 fish (Hartmana and Brandt, 1995a). Based on visual estimations of age 1 seasonal wet weights age one fish are growing at a slow rate (70-85gm). A positve trend is not evident for age 2 fish during the period. In fact, though sample sizes are small, mean starting mass (575gm) is greater than final mass (450gm). Patterns of condition denoted by flesh energy density (cal/gm wet weight) also suggest age-based differences in growth (see Hartman, 1993) which support field based growth estimates. Though flesh energy density of age 1 fish increase slightly (1393-1398) during the modeled period age 2 and > 3 fish show steady declines (1787-1695 and 1880-1865 respectively). Given age composition and distribution of striped bass (Appendix 7) included in spring model these growth and conditon trends support model predictions in that they show the same general trends.

During the fall modeled period (Julian day 267-322) seasonal wet weights reported by Hartman Brand (1995a) showed very little variation in mean mass. Growth of older fish (age 3 and four) provided evidence for postive growth rates. Energy densities of age 2 fish (Hartman, 1993) demonstrated trends, which nearly mimic growth model predictions temporally. Flesh energy initially declines but recovers by mid-period and then maintains a positive rate for the remainder (Hartman, 1993) of the period. Energy densities of age > 3 fish show continual decline throughout the period and suggest condition recovery after day 345 (Hartman, 1993). Growth models in this study included age 2 and ≥ 3 fish and predicted recovery occurring around day 282.

The average weight of an age 1 bluefish entering the Bay in May at approximately 400gm is approximately 900gm by Julian day 322 according to samples gathered randomly from the mid-bay and Patuxent Rivers by Hartman and Brandt (1995a). The same fish reached a mass of 1241gm by November based on littoral nocturnal rations, a mass very close to that reached by the largest age 1 bluefish sampled by Hartman and Brandt (1995a) during the same month (Appendix 18). If the same fish exited the Bay, as the catch data indicated most do, in late September an emigration weight of 1409gm is predicted to result. Unpublished research currently being conducted at the Virginia Institute of Marine Science (Bonzek, personal communication) provided field-determined weakfish growth comparisons with fish that were randomly collected throughout the Bay. Small sample sizes reduced the validity of comparisons with Hartman and Brandt (1995a). The institute's average age 2 fish was 211gm in May and obtained a median weight of approximately 500gm by late October. The same 211gm fish was predicted to weigh 1025gm by September and 889gm by November based on littoral nocturnal rations (Appendix 19). The largest age 2 weakfish sampled in November had a mass of approximately 1000gm; therefore, the model is predicting a mass that is not unrealistic according to field data.

Effects of diel temperature refuge

For striped bass daytime residence of deep water habitats provided a considerable increase in predicted final mass (797 vs. 730 gm). When resident fish sought daytime refuge in deep water they lost 20% of their original mass, without temperature sanctuary loss increased to 27% (Table 4.5). The energetic advantages

Table 4.5: Diel migrations to deeper waters were hypothesized based on vast differences in piscivore abundances between diel and nocturnal catches. Table 4.5 illustrates the predicted energetic cost of remaining in warm littoral waters during the day in terms of predicted growth reductions (grams final weight). July mass marks the end of the spring striped bass model and November marks the end of the fall model. Pr3edicted final mass of bluefish and weakfish at September and November emigration dates is given for comparison because both species growth curves indicate an optimum time of departure in late September. Remaining in shallows during warm daylight hours resulted in energetic losses for all species regardless of season or emigration date but extent of effect varied species-specifically.

Model	**Diel occupation of deep waters**	**July Mass (gm)**	**% Change**	**November Mass (gm)**	**% Change**
Striped Bass Spring	yes	797	n/a	n/a	n/a
Striped Bass Spring	no	730	-8.4	n/a	n/a
Striped Bass Fall	yes	n/a	n/a	1145	n/a
Striped Bass Fall	no	n/a	na	1144	< - .001
Model	**Diel occupation of deep waters**	**September Mass (gm)**	**% Change**	**November Mass (gm)**	**% Change**
Bluefish	yes	1409	n/a	1241	n/a
Bluefish	no	1188	-15.7	1048	-15.6
Weakfish	yes	1025	n/a	889	n/a
Weakfish	no	924	-9.9	801	-9.9

provided by cooler deeper habitats, though meager compared to the growth augmentation bluefish realized, may be more advantageous to striped bass production because these waters provided energy savings at a critical time when metabolic stresses caused by warming waters resulted in physiological stresses that were detrimental to striped bass condition. Deeper waters did not provide significant thermal advantages in the fall because shallow waters were rapidly cooling.

Bluefish and weakfish can augment energy acquisition by diel migrations to thermal refuges. Daytime immigration to cooler waters increased bluefish growth by 16% (1409 vs. 1188gm) if they departed in late September and by 16% (1241 vs. 1048) if they waited until November. Weakfish benefited substantially from diel migrations. Growth regardless of emigration date improved by 10% (1025 vs. 924gm, by Sept. and 889 vs. 801gm by Nov.)(Table 4.5). Equal improvement regardless of departure date suggests that thermal energetic advantages in deep-water were realized before September.

Sensitivity results

Sensitivity analyses were performed on the RA and RB's inputs of the respiration equation to determine effect on growth. Evacuation rates for each functional group were also examined. Unique species-specific growth curves required different methods of determining response to parameter alterations. Only terminal estimates were examined for striped bass because there were no seasonal apexes in projected growth. Maximum (early emigration) and terminal (late emigration) growth predictions were examined for bluefish and weakfish, however, because there is some question as to when emigration occurs and this timing has an effect on final weight.

Striped bass

Spring

RB variation affected final predicted mass of striped bass most significantly. Increasing RB reduced mass by 15% and reducing RB increased mass by 13%. RA increases also changed predicted mass by 11% and reduction by 12%. Striped bass were most sensitive to alterations in big crustacean's evacuation rate. Increases resulted in a 2% increase in mass and reductions resulted in an equal reduction in mass (table 4.6).

Fall

The fall striped bass model was not as sensitive to metabolism parameters. This finding reflects stress reductions associated with cooling water temperatures. RB alterations were again most sensitive but increases only reduced final mass by 8% and reductions increased it by 7% (table 4.7). Reductions in RA increased mass by 6%, and increases reduced mass by 7%. The most sensitive prey groups in the fall were big fish (gizzard shad) and small fish. Increasing big fish evacuation rate positively

Table 4.6: Table 4.6 is the spring sensitivity matrix for striped bass. It includes effects on growth due to metabolism and prey evacuation rate alterations. Emigration date in July is based on field data.

Spring Striped Bass Sensitivity Matrix			
Metabolism			
Parameter	Emigration	mass (gm)	% change
RA + SE	July	709	-11.0
RA - SE	July	896	12.4
RB +	July	681	-14.6
RB -	July	904	13.4
Prey evacuation rates			
Parameter			
shrimp + 10%	July	799	0.3
shrimp - 10%	July	795	-0.3
polychaete +	July	805	1.0
polychaete -	July	789	-1.0
fish +	July	803	0.8
fish -	July	791	-0.8
small crustaceans +	July	798	0.1
small crustaceans -	July	796	-0.1
big crustaceans +	July	814	2.1
big crustaceans -	July	780	-2.1

Table 4.7:Table 4.7 is the fall striped bass sensitivity matrix that contains the effects of metabolism and evacuation rate alterations on growth. The fall is a period of striped bass littoral immigration. Final mass resulted at the study's end not species' emigration.

Fall Striped Bass Sensitivity Matrix			
Metabolism			
Parameter	Project's end	mass (gm)	% change
RA + SE	November	1073	-6.3
RA - SE	November	1221	6.6
RB +	November	1050	-8.3
RB -	November	1227	7.2
Prey evacuation rates			
Parameter			
shrimp + 10%	November	1145	0.0
shrimp - 10%	November	1144	-0.1
polychaete +	November	1145	0.0
polychaete -	November	1145	0.0
big fish +	November	1175	2.6
big fish -	November	1115	-2.6
fish +	November	1163	1.6
fish -	November	1126	-1.7
big crustaceans+	November	1153	0.7
big crustaceans -	November	1137	-0.7

altered final mass by 3% and rate reduction decreased mass by 3%. Small fish or in this case all other fish species were less important. Rate augmentation and reduction increased and decreased predicted mass by 2% respectively.

Bluefish

The effects of RA and RB on bluefish varied according to emigration time. RB alterations in either direction removed the previous September mass apex. Increasing RB drove the fish to an eventual catastrophic weight loss (97%) and decreasing RB augmented growth by 331% in November (Table 4.8). A peak mass in September did result when RA was reduced and mass increased by 28%. Final mass in November increased by 36%. Fish were the most sensitive prey group. Augmenting the evacuation rate increased September mass by 29% and reductions decreased it by 22%. Final mass was increased by 32% and reduced by 25%.

Weakfish

The weakfish model was less sensitive to RB than RA (Table 4.9). Reductions in RA increased September mass by 42% and November mass by 54%. Increasing RA reduced predicted September mass by 29 and 35% respectfully. RB augmentation decreased early migration mass by 30% and late migration mass by 36%. Reduced RB estimates increased early migrants mass by 36% and late migrants mass by 46%. Weakfish were most sensitive to alterations in the rate of small fish evacuation. Rate augmentation increased predicted final mass regardless of emigration date. September emigration mass was predicted to increase by 28% and November mass by 31%. Reductions in small fish evacuation rate resulted in nearly equal decreases in emigration mass of 22 and 24% respectively. The relatively large alterations in predicted September and November emigration mass reflect the increased importance of small fish (anchovy) in the fall diet.

Table 4.8: Table 4.8 is a sensitivity matrix for bluefish that includes the effects of metabolism and evacuation rate alterations on growth according to emigration date.

Bluefish Sensitivity Matrix

Metabolism

Parameter	Emigration	mass (gm)	% change	Emigration	mass (gm)	% change
RA + SE	September	1096	-22.21	November	913	-26.43
RA - SE	September	1814	28.74	November	1686	35.86
RB +	September	400	-71.61	November	38	-96.94
RB -	September		0.00	November	5354	331.43

Prey evacuation rates

Parameter						
shrimp + 10%	September	1471	4.40	November	1295	4.35
shrimp - 10%	September	1350	-4.19	November	1188	-4.27
polychaete +	September	1416	0.50	November	1246	0.40
polychaete -	September	1403	-0.43	November	1235	-0.48
fish +	September	1811	28.53	November	1644	32.47
fish -	September	1097	-22.14	November	936	-24.58
small crustaceans +	September	1410	0.07	November	1241	0.00
small crustaceans -	September	1409	0.00	November	1240	-0.08
big crustaceans+	September	1457	3.41	November	1284	3.46
big crustaceans -	September	1366	-3.05	November	1199	-3.38

Table 4.9: Table 4.9 is a sensitivity matrix of weakfish that includes the effects of metabolism and evacuation rate alterations on growth according to emigration date

Weakfish Sensitivity Matrix

Metabolism

Parameter	Emigration	mass (gm)	% change	Emigration	mass (gm)	% change
RA + SE	September	726	-29.17	November	579	-34.87
RA - SE	September	1451	41.56	November	1366	53.66
RB +	September	714	-30.34	November	567	-36.22
RB -	September	1396	36.20	November	1302	46.46
Prey Evacuation Rates						
Parameter						
shrimp + 10%	September	1060	3.41	November	919	3.37
shrimp - 10%	September	987	-3.71	November	855	-3.82
polychaete +	September	1067	4.10	November	925	4.05
polychaete -	September	980	-4.39	November	850	-4.39
big fish +	September	1036	1.07	November	905	1.80
big fish -	September	1011	-1.37	November	872	-1.91
small crustaceans +	September	1027	0.20	November	890	0.11
small crustaceans -	September	1019	-0.59	November	883	-0.67
big crustaceans+	September	1039	1.37	November	905	1.80
big crustaceans -	September	1007	-1.76	November	869	-2.25
small fish +	September	1312	28.00	November	1163	30.82
small fish -	September	798	-22.15	November	676	-23.96

DISCUSSION

Bioenergetic models of striped bass, bluefish, and weakfish growth based on field derived nocturnal consumption estimates suggest that vegetated mesohaline littoral zones are highly beneficial to bluefish and weakfish but metabolically challenging to striped bass during warm water conditions. Bluefish and weakfish models based on average nocturnal ration predicted that fishes foraging in littoral zones attained improved growth rates compared to other bluefish collected from across a conglomerate of habitats in the Patuxent River and northern mainstem of the bay (Hartman and Brandt, 1995a) and weakfish collected randomly from across all of the Bay's habitats (Bonzek et al., unpublished). Large differences in modeled and field determined growth rates might be the result of inaccuracies due to data collection or model construction. It is equally plausible, however, that the increased prey diversity and biomass found in vegetated littoral zones augmented predator energy acquisition. If the expanded diversity and biomass of prey resources provide in littoral zones increases trophic energy exchange to upper level fishes, historic reductions in the quantity and quality of vegetated littoral habitats may have had several negative affects on that production. Habitat reductions may have resulted in an increased trophic dependence on pelagic sources, augmented trophic overlap, and possibly even limited the bay's upper level fish production capacity. Investigations into the potential affects of diel migration to deep-water habitats during warm daylight hours suggest that these thermal refugia can provide substantial benefits to all three piscivores. Bluefish and weakfish achieved improved growth and resident striped bass reduced physiological stresses and energetic losses caused by extended exposure to high water temperatures.

In order for net predator production (growth and reproduction) to increase, energy uptake must exceed that required for assimilation and metabolism (Valiela, 1995), if net energy becomes negative weight loss and reduced condition will result. Summer growth depression or weight loss is not unusual for fishes and has been reported by other investigators for various estuarine species (Wohlschlag et al. 1968; Wohlschlag and Wakeman, 1978; Cech and Wohlschlag, 1975). The models of this study stress how important physical habitat parameters are to metabolic functions.

Striped Bass Growth

Striped bass are physiologically ill suited for the high water temperatures found in lower Chesapeake Bay littoral zones during summer months. Their physiology provide for maximum growth around 15C and above 25-28C, a temperature common during the study period, a marked decline in growth occurs (Hartman and Brandt, 1995b). The lower thermal optima, narrower scope for growth (Coutant et al 1984; Coutant, 1990; Brandt et al. 1992), and a reduced average daily ration acquired by (C/C max) striped bass resulted in net weight loss by striped bass throughout warm water periods.

The initial growth of striped bass (<711) in cool waters of early spring and of larger fish (> 406 gm) in the fall suggests that Chesapeake's littoral habitats can at times be hospitable to striped bass growth. Unfortunately, metabolically advantageous temperatures for the species were short lived during the selected study period. Striped bass that remained into late spring consistently experienced temperatures above 25C the threshold that marks growth deterioration (Hartman and Brandt, 1995b). In addition, during these warm periods food acquisition (C/C max) declined. Though deeper waters may provide energetic savings these benefits were not enough to offset energetic cost. Overwhelming energetic expenses lead to weight loss and a presumed decline in physical condition, a physiological condition that would make the fish more susceptible to infection and disease.

When water temperatures returned to levels below 20C in the fall the C/C max ratio showed marked augmentation and striped bass physical condition indicated by growth rates rebounded. Similar seasonal patterns in striped bass flesh energy density (Hartman, 1993) also provide evidence that seasonal temperature changes affect striped bass condition and suggest that the degree to which temperature affects the physiology of the species varies with ontenogenic alterations.

Larger fish (age 2 and 3) show seasonal energy density y declines that correspond to water temperature alterations. Age 2 fish flesh condition began to decline in mid-April and continued until late October (Hartman, 1993). This result mimics growth predictions of both spring and fall models. Hartman (1993) found that Age 3 fish condition continued to decline until late November. The fall striped bass model of this study suggests a slightly earlier recovery (mid-October) by age 3 fish. Differences in timing may be an artifact due to extrapolation between sampled energy densities (Hartman, 1993), actual differences between sampled habitats prey provisions in northern bay and southern littoral zones, and/or the inclusion of larger migratory fish in southern littoral samples that did not endure seasonal loss in condition.

Though similar seasonal patterns were denoted by degradation in flesh energy density (cal/gm wet weight) for age-2 and > 3 fish, age 0 and age 1 maintain positive growth throughout warmer water periods (Hartman, 1993) in the upper bay. Age specific habitat requirements are known to be important to various marine species especially anadromous and catadromous fishes. Understanding the habitat requirements of species with complicated life histories and age-based physiological deviations in responses will require more through physiological work in order to provide applicable indices to determine age-specific essential fish habitats. A good example of size-specific (a proxy for age) habitat value is provided in the current study's fall growth model. Growth was due in large part to consumption of gizzard shad that due to their size were not trophically available to smaller younger fish. The habitat was more tropically beneficial to larger fish simply due to available prey size.

Over the past decade striped bass condition indices along the Atlantic coast have been in decline (Overton et al. 2000). This has lead some researchers to suggest that reduced weight –length relationships and skin lesions found on some fish are the result of reduced prey availability (Uphoff, 1998; Overton et al. 2000). In this study, though prey availability was positively correlated with water temperature (Appendix 2) and the percentage of C max consumed by striped bass was generally inversely related to water temperature. In contrast, higher water temperatures had no significant effect on bluefish and weakfish that regularly consumed a majority of maximum daily ration (Hartman and Brandt, 1995b) during nocturnal feeding forays throughout the summer. Reduced striped bass consumption ratios despite adequate prey resources support Coutant's (1985) speculative hypothesis that physiological stresses reduce effective foraging. Declines in flesh energy densities (a proxy for condition) in age 2 and 3+ fish collected in the field during warm water months by Hartman (1993) also provide evidence of declining condition with increasing temperature and energy content recovery following cool water periods. These trends are mimicked by model predictions during the same periods. It is interesting to note that growth recovers, despite reduced prey resource availability, which adds further support to the theoretical linkage between feeding success and temperature.

When metabolic costs outweigh benefits striped bass migrate to stay in a water body that contains the preferred body temperature (Coutant, 1986; DeVries, 1982). As long as water temperatures remain within tolerable boundaries (Coutant et al 1984; Coutant, 1987, 1990), however, striped bass will take advantage of profitable feeding conditions. In cooler northern waters, striped bass have been found to feed throughout the summer during daylight hours even on low water conditions (Tupper and Able, 2000; Nemerson and Able, 2003). The results of these various investigators suggest that habitat quality in terms of physical character (thermal) and productivity (prey resources) is an important factor currently affecting striped bass condition and health.

Compensatory Growth

Alternate periods of intense growth and famine are very common in the natural environment; in fact some fish achieve improved net growth when subjected to such alternating conditions (Smith, 1981; Dobson and Holmes, 1984; Miglavs and Jobling, 1989 a, b). This metabolic response often referred to as "compensatory growth" has also been observed in other vertebrates (Wilson and Osborne 1960; Bilton and Robins, 1973) and invertebrates (Perrin et al. 1990; Bradley et al. 1991). Despite the wide spread nature of this response and its potential consequences on population and ecosystem dynamics the physiological and behavioral mechanisms underlying such growth are poorly understood (Broekhuizen et al. 1994). In general, the response has been examined based on food availability and in part this is the problem facing resident striped bass. Many predatory species are known to endure long periods of food shortage and thus declining physical condition during winter months (Larsson and Lewander, 1973; Hawkins et al. 1985; Schultz, 1996; Hurst and Conover, 2001). This study suggests a similar life cycle for resident striped bass though the energetic expenses are associated with possible food shortages and increased metabolic cost due to warm water conditions. It may be that, evolutionarily, the energetic cost of summer residence is less detrimental than predation risk associated with oceanic migration for smaller fishes. This hypothesis would be greatly supported and energetic losses minimized if the species' was capable of compensatory growth when cooler water temperatures return to the Bay.

Parameter Uncertainty

Parameter uncertainty is an area of primary concern in bioenergetic model application (Hansen et al. 1993); the importance of this uncertainty is increased when models are used to predict energetics of fishes operating at or near their thermal limit. Small changes in the temperature that supports positive growth can result in large changes in growth potential (Kitchell et al. 1974, Brandt et al. 1991, 1992). Ontogenetic differences exist that alter the metabolism and thus thermal optima for growth in striped bass (Coutant et al 1984;Coutant, 1990; Brandt et al. 1992). Hartman and Brandt's (1995b) comparison between the scope for growth of a standardized 30gm fish and a 1000gm fish indicate that maximal growth temperature declines with fish size and that smaller fish are capable of sustaining higher growth rates at higher temperatures. Metabolism parameter values supplied by Hartman and Brandt (1995b), however, force a choice between age-0 fish (30gm) and all older fish (standardized sizes from 100-1000gm). This oversimplification omits possibly significant ontogenetic factors that may allow for improved growth of smaller resident fish in our study site. Feeding studies across greater temperature variations and ontogenetic stages need to be conducted to clarify effects on metabolism and scope for growth. These studies can supply the needed information on thermal optima and compensatory growth thus helping to clarify the energetics of resident striped bass.

In the spring striped bass model inputs were included that need to be discussed because of their possible effects on estimation of energetic losses. First, the size range of striped bass varied greatly throughout the study period (Appedix 6) and size diversity declined during the spring period due to emigration. When stomach content was attained, 50 fish were randomly selected within each catch. Catches were not separated into size classes because sample size prevented such separation without complete retention, which would have resulted in total mortality. This collection method limited knowledge of stomach content within specific size classes and prevented the creation of possibly more accurate size based models. Second, as mentioned previously, striped bass energy densities entered into the respiration equation fluctuate seasonally (Hartman, 1993) and during the spring model they are in constant decline. Declining condition is likely due to physiological stresses caused by increasing water temperatures and poor consumption. These variables and their impact on growth are already being included as model parameters; therefore, noting both cause (temperature and C/C max) and effect (flesh energy content) may have created a feed back mechanism that falsely exacerbated energetic losses.

Bluefish and Weakfish Growth

Ontogenetic differences in thermal optima for bluefish and weakfish were not found by Hartman and Brandt (1995b), thus alleviating potential uncertainty in this parameter's estimation. Bluefish's and weakfish's scopes for growth were not metabolically restricted by warmer littoral waters, an advantage that enabled them to take advantage of the increased prey abundance and diversity provided during warm water months. The specific growth rates of both piscivores continue to improve far beyond the 15C optimal temperature that restricted striped bass growth. Adult bluefish growth rate increase rapidly until about 23C and the fish does not suffer from temperature stress until over 28C and then the rate of decline is slight (Hartman and Brandt, 1995b). Adult weakfish have a similar metabolic response to increased temperatures; specific growth rate increases until 25C and declines very slowly above that temperature (Hartman and Brandt, 1995b). Metabolically, these fish were much better suited to the warm littoral waters that prevailed during their residence within the study period.

During the study period, the bluefish C/C max ratio recorded was not as high as their weakfish competitor. Actual consumption, however, was underestimated due the bluefish habit of regurgitation upon capture. Despite this restriction predicted bluefish growth was greater than weakfish a result that was likely due to the increased scope for growth bluefish are capable of at higher temperatures. Growth predictions suggest that littoral habitats are highly beneficial to young bluefish. Littoral nocturnal rations provided improved growth rates in comparison to fish feeding across all upper bay habitats (Hartman and Brandt, 1995a) regardless of diel thermal refuge use.

Adult weakfish are generally considered demersal predators often associated with deep channel habitats (Chesapeake Bay Program Weakfish and Spotted Trout Fishery Management Plan 1990). This perception may be due to the fact that weakfish are well adapted to pelagic predation and are often found suspended in cool deep waters during the summer when low dissolved oxygen levels drive other fishes out of the depths (Chao and Musick, 1977). Commercial landings, however, paint a different picture of this predator. The weakfish is the third most often caught species in Virginia's commercial haul-seine fishery (VMRC, 2003), a fishery that only operates in shallow water. Historically, when weakfish biomass was greater, the species played an even larger role (Hilldebrand and Shroeder, 1928). Commercial landings and the behavioral and dietary observations done by Lascara (1981) suggest that adult weakfish forage along eelgrass beds (Chesapeake Bay Program Weakfish and Spotted Trout Fishery Management Plan 1990); therefore, littoral habitat composition and provision of prey may be far more important to the production of this species than previously suspected.

Weakfish were the only piscivore whose nocturnal ration surpassed predicted maximum daily ration (Hartman and Brandt, 1995b). Surpassing estimated C max would at first seem problematic. Further examination of the methods used to determine C max (Hartman and Brandt, 1995b) and comparisons with other studies, however, suggest that consistently high C/C max ratios only mark how trophically beneficial the zone was to the species. Hartman and Brandt (1995b) estimated average C max based on point estimates of maximum consumption as determined in laboratory feeding experiments. These point estimates may not reflect average daily rations in the field or over longer periods of time (see Smagul and Adelman, 1982; Trudel and Boisclair, 1993). Though field studies of minnows have found low daily variation (7-16.3%) in daily ration (Trudel and Boisclair, 1993) much larger variations in daily ration (30-40%) have been found for higher-level fish (Smagula and Adelman, 1982). Even larger variations existed between individual fish and the mean maximum consumption (11-205%) and mean maximum ration (29-142%) determined in ht laboratory by Hartman and Brandt (1993).

In addition, field determined weakfish diet composition in this study was highly varied seasonally. Hartman and Brandt's C max estimates were based on three prey types, which were fed to fishes in small portions. Since different prey types likely yield different C max functions with very different magnitudes, substantial differences in consumption in the field may represent varied diets (Hartman and Brandt, 1993). Field ration estimates likely vary considerable from those determined in the laboratory because consumption is strongly influenced by predator-prey encounter rates, which in turn are a product of various environmental factors including prey densities (Breck, 1993). Variability in consumption among piscivores may be so large that it must be established through field estimates if its impact on total energy budget is to be properly understood (Armstrong, 1986; Lucas and Armstrong, 1991).

Unpublished research currently being conducted at the Virginia Institute of Marine Science (Bonzek, personal communication) provided field-determined weakfish growth comparisons with fish that were randomly collected throughout the Bay. Small sample sizes reduced the validity of comparisons with Hartman and Brandt (1995a). The institute's average age 2 fish was around 211 gm in May and obtained a median weight of approximately 500gm by late October. The same 211gm fish is predicted to weigh 1025 gm by September and 889 by November based on littoral nocturnal rations.

By staying in littoral zones after September, bluefish and weakfish experience a theoretical loss of weight. Modeled energetic losses after September may suggest that there is an optimal time for emigration, which may be linked to prey resource availability, increased competition from immigrating striped bass, and/or temperature affects. Fall condition deterioration may also be an artifact caused by reduced sample sizes that were inadequate to estimate daily ration. Larger sample sizes and relatively high consumption ratios for weakfish during the period suggest that predicted reductions in condition might be primarily the result of rapidly falling water temperature.

Growth estimations of the weakfish model do not include a pathway to account for energetic cost of reproduction. This could lead to overestimation of final mass because weakfish spawn in near shore and estuarine waters during the study period with peak occurrence in late April to June (Mercer 1983). In order to account for reproductive energetic cost and to provide better comparisons with field-determined estimates of growth that inherently include such losses; gonadal development energetic cost must be subtracted from predicted growth. Predictions of final mass should be reduced by about 13% for adult females and 5% for adult males (Toetz, 1971). Assuming an equal distribution between sexes gonad weight would be 9% of mass. This lowers predicted September mass to 933gm and November mass to 809 gm. These masses are still noticeably higher than the median growth determined from fish sampled randomly across habitats.

Thermal sanctuaries

A habitat's energetic value need not be trophically based though this was the expected benefit to be realized in littoral zones filled with suitable prey items. Environmental temperature fluctuations are of crucial importance to fishes because they are cold-blooded, which links their metabolism and energy budget directly to external controls (Brett and Groves, 1979). The effects of seasonal temperature fluctuations on fish immigration and emigration in the Bay are well recognized (Hildebrand and Shroeder, 1928; Chao and Musick, 1977; McBride and Conover, 1992; Murdy et al., 1997) presumably this seasonal temperature selection behavior places a species at the temperature at which it functions most efficiently (Evans, 1993). Although most fish are able to thermoregulate to some degree by behavior alterations and microhabitat selection, this approach may not be effective in dealing with long-term diurnal, seasonal or evolutionary alterations (Evans, 1993).

When metabolic cost due to temperature exceed trophic benefits, a species must migrate to a water body that provides more appropriate environmental conditions. This hypothesis has been applied to explain striped bass summer migration (Coutant, 1986). Frequency distributions of temperature data transmitted from free-swimming striped bass confirm that fish will occupy a progressively deeper position in order to stay in a more physiologically pleasing temperature within an experimental quarry as summer progresses and surface temperatures rise (Coutant, 1987). Striped bass migrations also appear to be directed movements motivated by staying in a water body containing the preferred body temperature (Coutant, 1986; DeVries, 1982). This study's catch data also suggest that striped bass actively avoided littoral zones during the warmest periods of the study. Only one striped bass was captured in the study site during mid-summer and none were taken during late summer-early fall when water temperatures reached an apex. If migration does not occur and no suitable temperature regime can be found, the fish can only attempt to gather enough prey to make up for its energetic losses and wait for cooler temperatures to return.

Littoral zone water temperature can fluctuate significantly on a diurnal cycle and reach extremely high or low temperatures seasonally. The temperature of deeper waters is less erratic and seasonally lags behind that of the shallows. Temperature variations due to depth and this lag may provide short-term thermal sanctuaries that fish use to their advantage. It is physiologically possible and evolutionarily probable that fish seek out habitats that accentuate energy acquisition and/or minimize losses. Day night catch comparison provided by field data collected during this study suggest that after obtaining prey in littoral habitats nocturnally, highly mobile fishes, known to travel on the tidal cycles (Chao and Musick, 1977), seek out deeper waters with more profitable thermal conditions that optimize metabolic gain.

Models that compared growth rates of fish exposed to deep-water temperatures and littoral temperatures during daylight showed that bluefish and weakfish both benefited from theoretical occupation of thermal refugia during daylight. Deeper waters were cooler and thus more beneficial during the summer and warmer waters of early fall. Striped bass did not realize any advantage by entering deeper waters in the fall when littoral water temperature was more metabolically suitable. Striped bass benefited from deep-water sanctuaries in the spring model, which included early summer, but the percent change in predicted mass was less dramatic than the other two piscivores. Basing a habitat's contributions to a species on a change in growth percentage may be misleading. Striped bass were already experiencing a loss in condition. Energetic savings, though reduced in magnitude, may be more important for a species that is energetically suffering. Assuming thermal sanctuary model predictions of energetic savings are correct, deep-water habitats and the thermal sanctuaries they provide may be essential to resident striped bass due to energetic savings.

Other environmental attributes such as salinity may also make certain deep-water habitats more suitable thermal sanctuaries. Growth studies of many estuarine fishes including juvenile striped bass show lower metabolic rates, higher growth rates, and/or maximum growth efficiencies at mesohaline salinities (Otwell and Merriner, 1975; Hettler, 1976; Fanta-Feofiloff et al., 1986; Perez-Pinzon and Lutz, 1991). It is generally accepted that teleosts evolved from fresh water predecessors, and the fact that teleostean plasma NaCl concentration is 30% that of seawater supports this proposition (Evans, 1993). This difference in internal verses external salinity presents a problem of potential volume depletion and salt loading in marine environment that must be offset by osmoregulation. The cost of this regulation depends upon the electrochemical gradient between the fish and it's surrounding water (Evans, 1979; Potts, 1984). Energetic costs are positively correlated with increased differences in gradients therefore habitats that contain lower gradients provide increased energy savings. Estuarine dependent species face varying and opposing gradients on short time frames thus complicating their osmoregulatory problems. Anadromous fishes like the striped bass likely evolved more sophisticated methods to minimize energetic challenges of osmoregulation, but the metabolic consequences of this task and its possible links to ontogenetic alterations are not well understood and thus cannot be currently included in bioenergetic models.

Changes in the bay's physical environment other than temperature and salinity such as dissolved oxygen (Coutant and Benson, 1990; Pihl et al. 1991) likely influence piscivorous fish movements and may affect feeding behaviors (Pruell et al., 2003). When temperatures clime bass prefer to occupy the coolest water available with a dissolved oxygen concentration greater than 2.5 mg/L (Crance, 1984; Matthew et al. 1989). Dissolved oxygen has recently been found to be an important motivator of striped bass distribution (Schaffler et al., 2002).

Though anoxia has been observed in the Chesapeake since the 1930's (Newcombe and Horne, 1938) it has become more widespread and longer lasting in recent years (Flemer et al., 1983; Secor et al., 1998). If oxygen level is depleted in cooler waters bass are forced to occupy temperatures warmer than those in its preferred physiological range (Farquhar and Gutreuter, 1989; Zale et al. 1990) and condition deteriorates. Predicted warming trends, increased alteration of stream flows, and increased hypoxia are predicted to further restrict striped bass habitat suitability in the Chesapeake in coming years (Coutant, 1990). Because striped bass are not physiologically suited to warm waters decreasing coverage of suitable deep low salinity habitats will likely augment decline in condition and health. Anoxic events in the upper bay's deep-water habitats, which due to reduced temperature (Coutant, 1986; DeVries, 1982) and osmotic cost associated with increasingly fresh water (Otwell and Merriner, 1975; Evans, 1993) should provide the greatest benefit to summer resident striped bass, may be of particular importance.

The extent to which decreased production of bluefish and weakfish or current striped bass condition decline can be explained by alterations in the biological and physical character of the bay's habitats is unclear. What is obvious from model predictions is that littoral habitats provide better than average daily rations and that seasonally alterations in physical habitat conditions and species specific physiological characteristics that may be ontogenetically variable are important parameters that should be considered in definitions of essential fish habitats. Denying access to or destruction of habitats that provide better than average seasonal energetic advantages will result in less than average production and/or declining condition and increased susceptibility to health risk. Conditions similar to those witnessed in the bluefish, weakfish, and striped bass stocks (Overton et al., 2000).

Sensitivity analysis

Sensitivity analysis demonstrated how sensitive bioenergetic models are to parameters influencing respiration (temperature). Alterations to RA (intercept) and RB (R vs weight) based on adding and subtracting the error associated with the 95% confidence interval consistently had the largest effect on growth, with RB being the greater of the two. The degree of perturbation to final growth predicted varied between species with largest impacts realized in the bluefish model and smallest in the striped bass models. Bluefish were so sensitive to RB perturbation that reductions led to a quadrupling of final mass and increases caused catastrophic mass decline. Sensitivity analysis of the striped bass spring and fall models indicated the models were not as sensitive to RA and RB or digestion rates as bluefish or weakfish. Their lower thermal optima and narrower scope for growth at higher temperatures overwhelmingly restricted striped bass metabolism.

Sensitivity analysis of prey evacuation rates made interesting trends in resource use apparent across species. Bluefish and weakfish were most sensitive to alterations in fish evacuation. A 10% increase in fish evacuation resulted in a 29-32% change in final mass depending on whether emigration occurred in September or November. Decreases resulted in 22-24% reductions. The evacuation rate of small fish was most important to weakfish. Increases (28-31%) and decreases (22-24%) had similar affects on their final mass. Striped bass growth was an order of magnitude less sensitive to evacuation rate alterations. This is likely the result because striped bass consumption was so greatly reduced during the majority of the study period. An inhibition that may have been due to reduced forage success at higher water temperatures (Coutant, 1985). They were most sensitive to alterations in blue crab in the spring and fish in the fall. Increased sensitivity to fish evacuation rate alterations in the fall reflected an augmentation of dependence on fish by larger striped bass. This increase is due largely to the fact that larger fish can take advantage of the large gizzard shad abundant in the shallows.

Vita

Born in Richmond, Virginia, 19th of February 1966. Graduated from Hampton Roads Academy in 1984 and earned a degree at Washington and Lee University in History in 1988. Worked as natural resource professional for National Fish and Wildlife Foundation, Chesapeake Bay Foundation, and Virginia Marine Resource Commission from 1989- 93. Became registered commercial fisherman in 1993 and first Orvis endorsed Chesapeake Bay flyfishing guide in 1994. Received M.A. in Marine Science from College of William and Mary, Virginia Institute of Marine Science, department of fisheries in 2000. Entered doctoral program department of biology at same institute in 2000.

Appendix, Text, and Equations of Piscivores' Models

Appendix 1: The first table contains date specific data on mummichog gear efficiency estimates. The second contains species-specific information on other prey seine species. Size distribution represents both trials. The third table contains species-specific analysis of haul-seine.

Table 1.

Date	Tag location	Number tagged	% Recaptured	Water temp. (C)
06-Nov	Caudal	116	61	13
06-Nov	Dorsal	74	41	13
07-Nov	Caudal	115	60	13
07-Nov	Dorsal	80	46	13
03-Dec	Dorsal	150	81	9
03-Dec	Dorsal	130	78	9

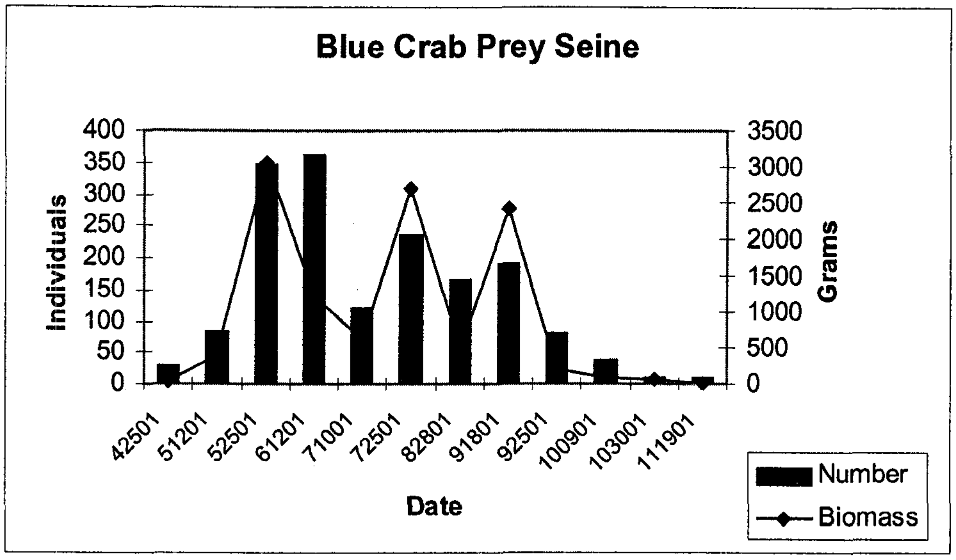
Table 2.

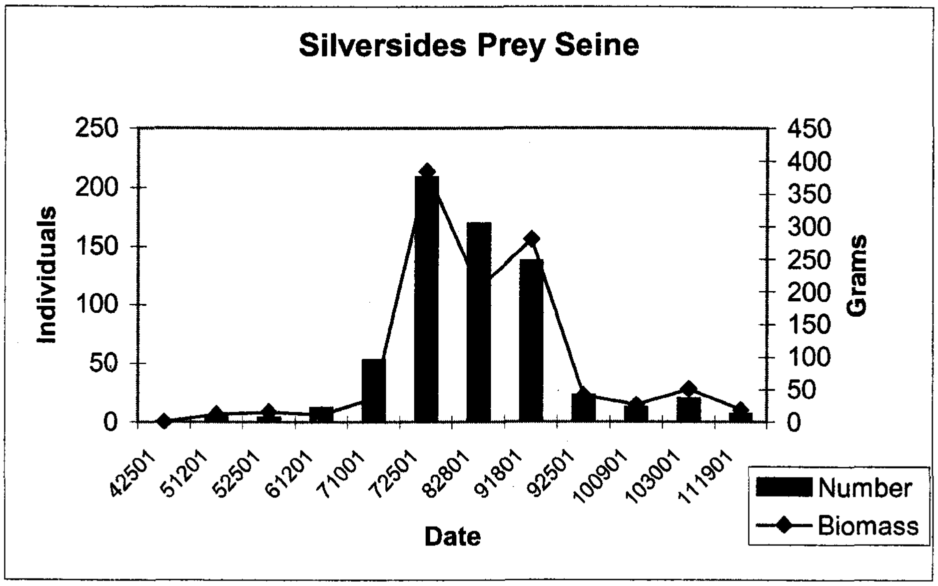
Date	Tag location	Species	Number tagged	Size Dist. TL (mm)	% Recaptured	Water temp. (C)
06-Nov	Dorsal	Striped Killifish	10	49-90	50	13
07-Nov	Dorsal	Striped Killifish	6	49-90	100	13
06-Nov	Caudal	Sheepshead	14	49-58	43	13
06-Nov	Dorsal	Atlantic silverside	20	65-100	65	13
07-Nov	Dorsal	Atlantic silverside	16	65-100	75	13
06-Nov	Dorsal	Red drum	11	43-72	73	13
07-Nov	Dorsal	Red drum	27	43-73	89	13
07-Nov	Dorsal	Spotted trout	2	110-163	50	13
06-Nov	Swimmer	Blue crab	6	25-75	33	13
07-Nov	Swimmer	Blue crab	10	25-75	40	13

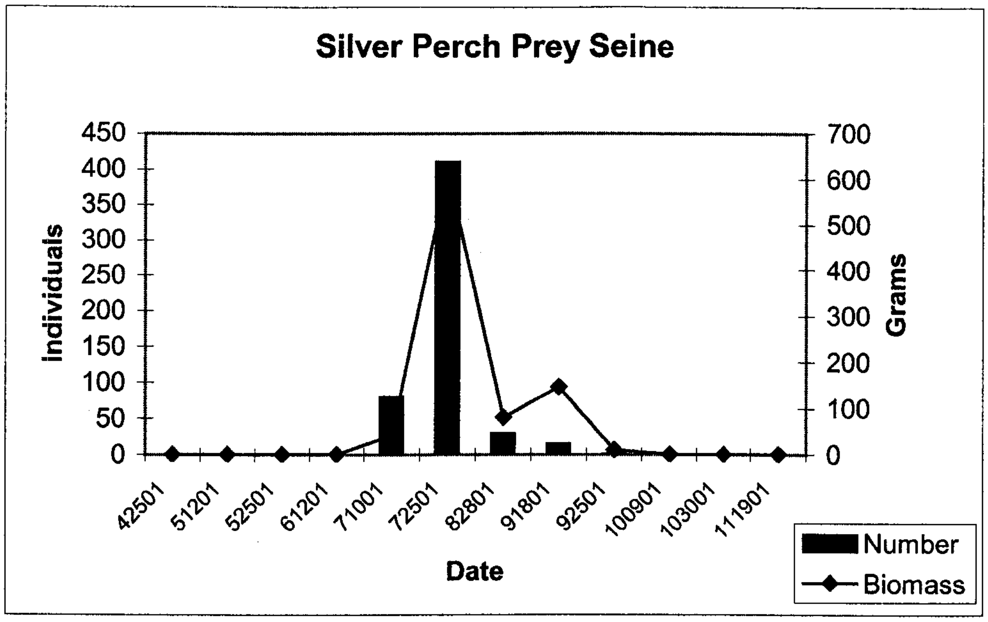
Table 3.

Date	Tag location	Species	Number tagged	Size Dist. Tagged TL (mm)	Size Dist. Recaptured TL (mm)	% Recaptured	Water Temp. (C)
03-Jun	Dorsal	Summer flounder	2	261-272	n/a	0%	22
03-Jun	Dorsal	Atlantic croaker	169	228-340	231-340	50%	22
06-Oct	Dorsal	Summer flounder	2	271-280	n/a	0%	20
07-Oct	Dorsal	Atlantic croaker	20	223-260	223-260	50%	20
08-Oct	Dorsal	Spot	53	183-303	196-303	62%	20
09-Oct	Dorsal	Pinfish	48	172-220	180-206	71%	20
10-Oct	Dorsal	Red drum	7	331-445	337-392	57%	20
11-Oct	Dorsal	Black drum	2	227-261	227	50%	20
12-Oct	Dorsal	Gizzard shad	30	237-465	325-398	43%	20
13-Oct	Dorsal	Sandbar shark	2	670-675	670-675	100%	20

Appendix 2: Appendix 2 contains charts of abundance and mass for the ten most abundant species captured in the prey seine. Abundance estimates do not include gear efficiency corrections.



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400
350
300
250
200
150
100
50
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Grams
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600
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100
0
42501
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71001
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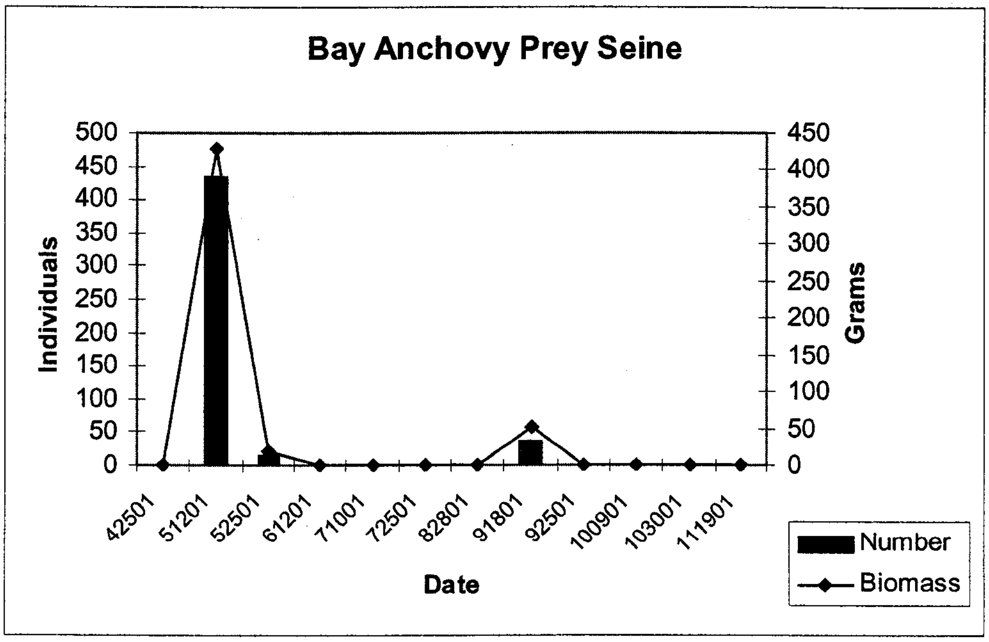
82801
91801
92501
100901
103001
111901
Date
Number
Biomass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400
350
300
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Grams
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250
200
150
100
50
0
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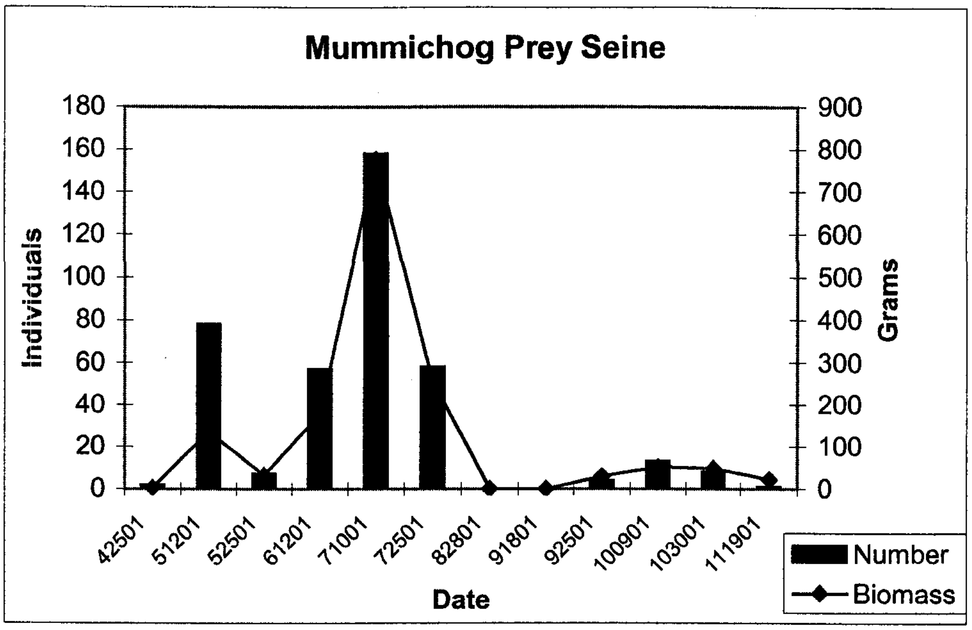
111901
Date
Number
Biomass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400
300
200
100
0
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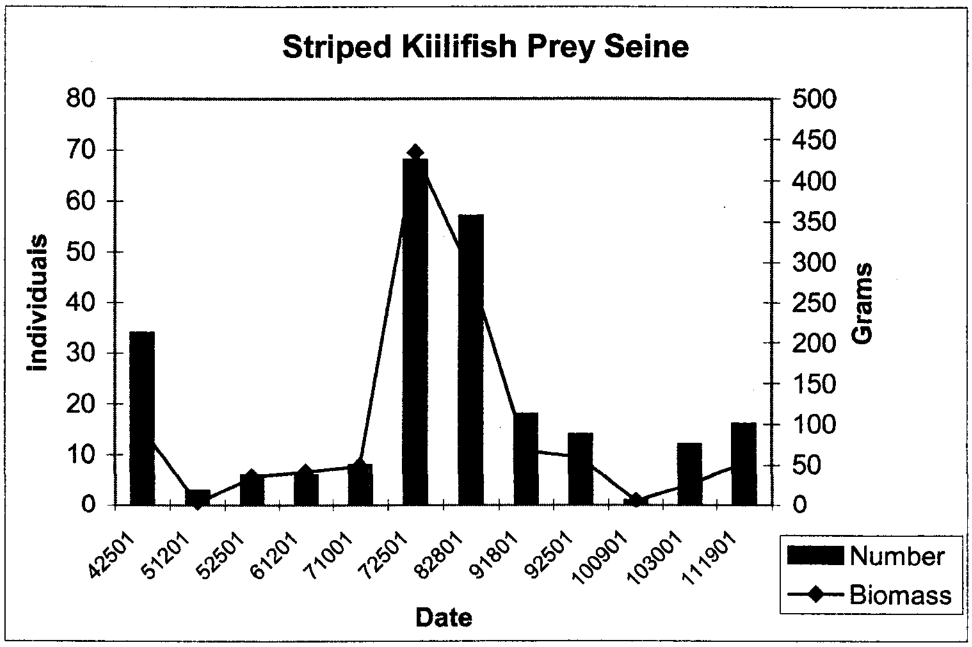
Date
Number
Biomass


Striped Kiilifish Prey Seine
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Grams
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250
200
150
100
50
0
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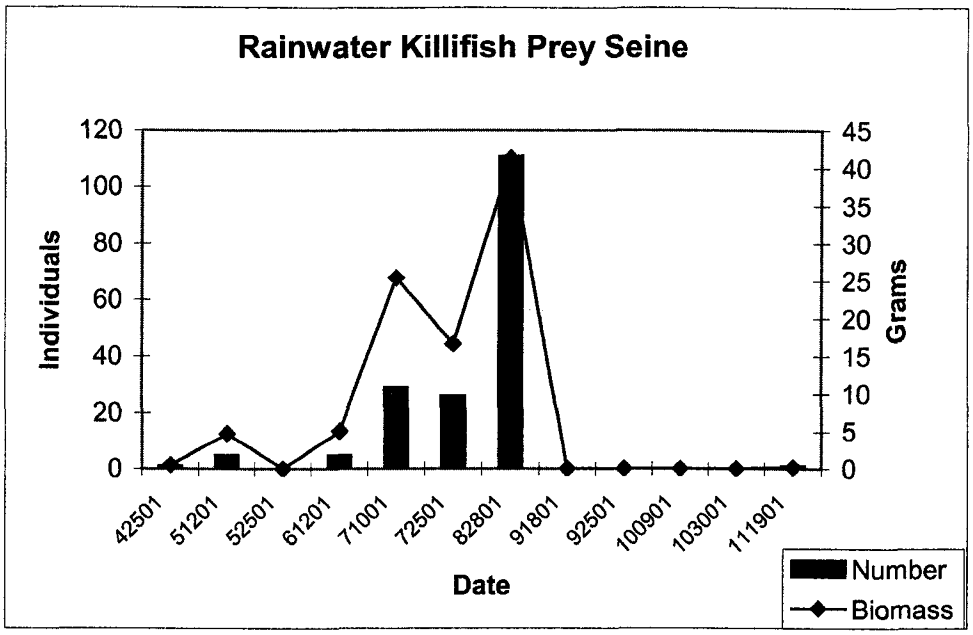
Date
Number
Biomass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Individuals
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60
40
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Grams
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15
10
5
0
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91801
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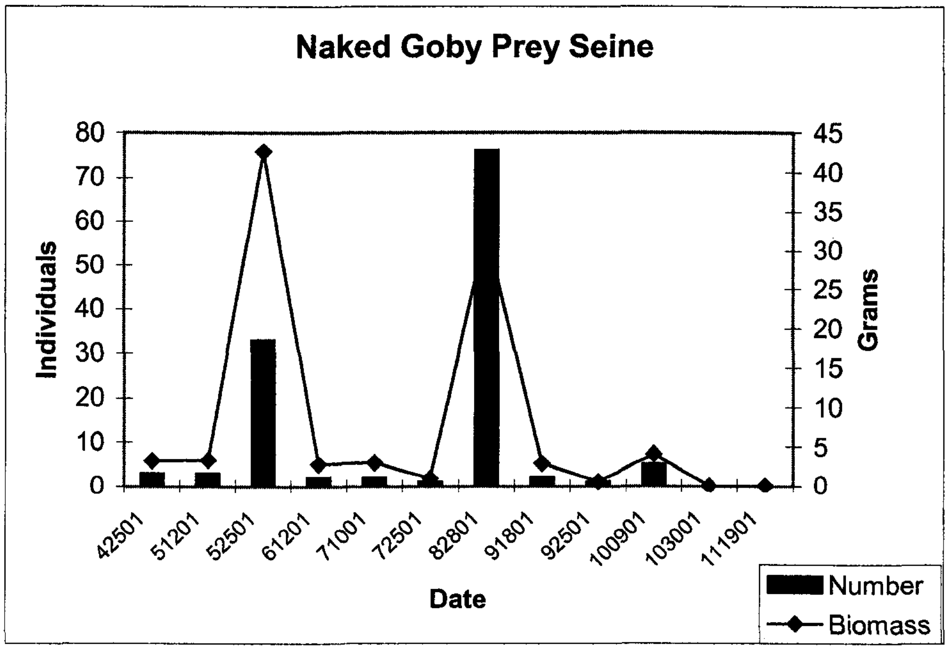
100901
103001
111901
Date
Number
Biomass


Naked Goby Prey Seine
Individuals
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50
40
30
20
10
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Grams
45
40
35
30
25
20
15
10
5
0
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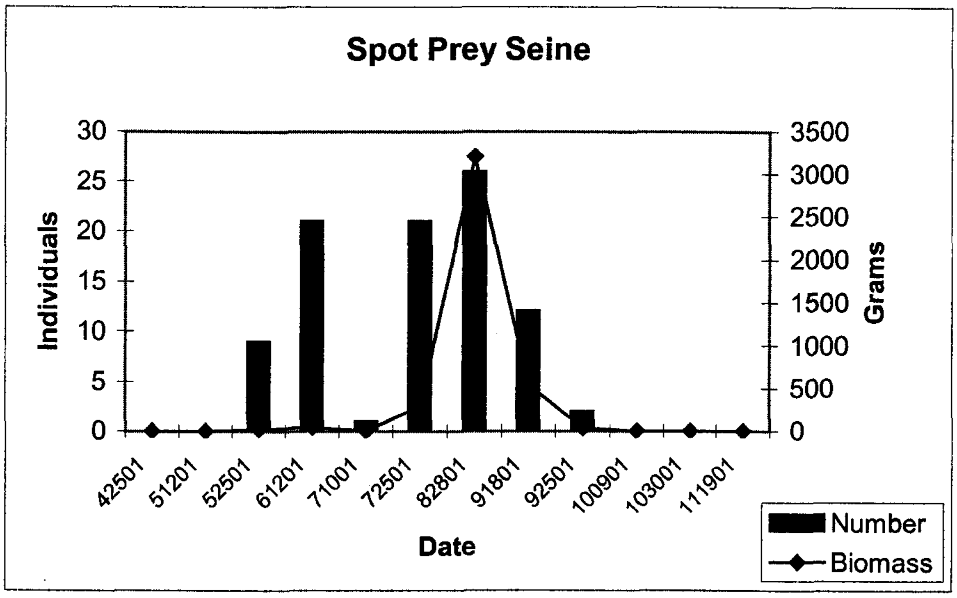
111901
Date
Number
Biomass


Spot Prey Seine
Individuals
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Grams
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2500
2000
1500
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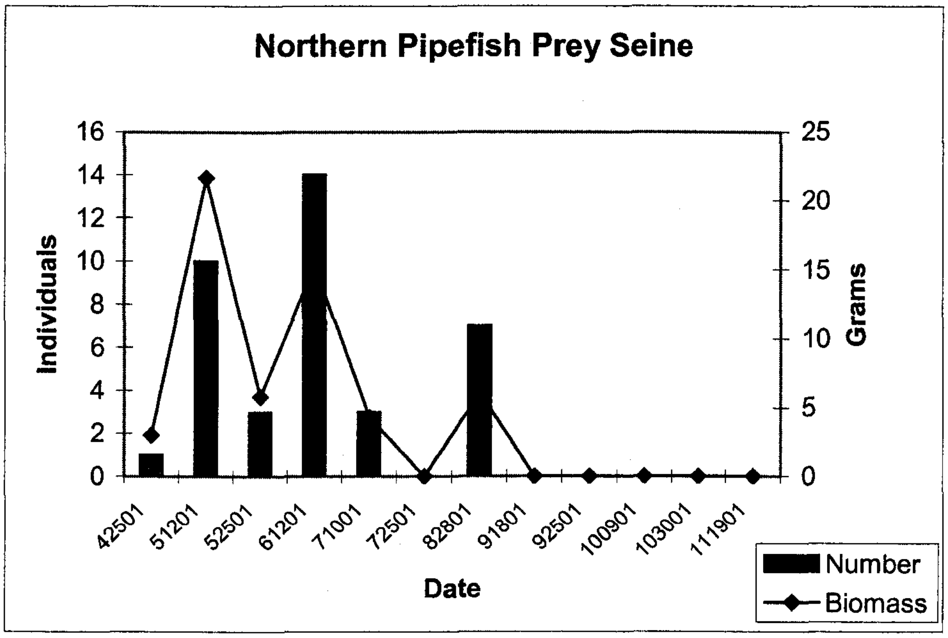
Northern Pipefish Prey Seine
Individuals
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14
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8
6
4
2
0
Grams
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10
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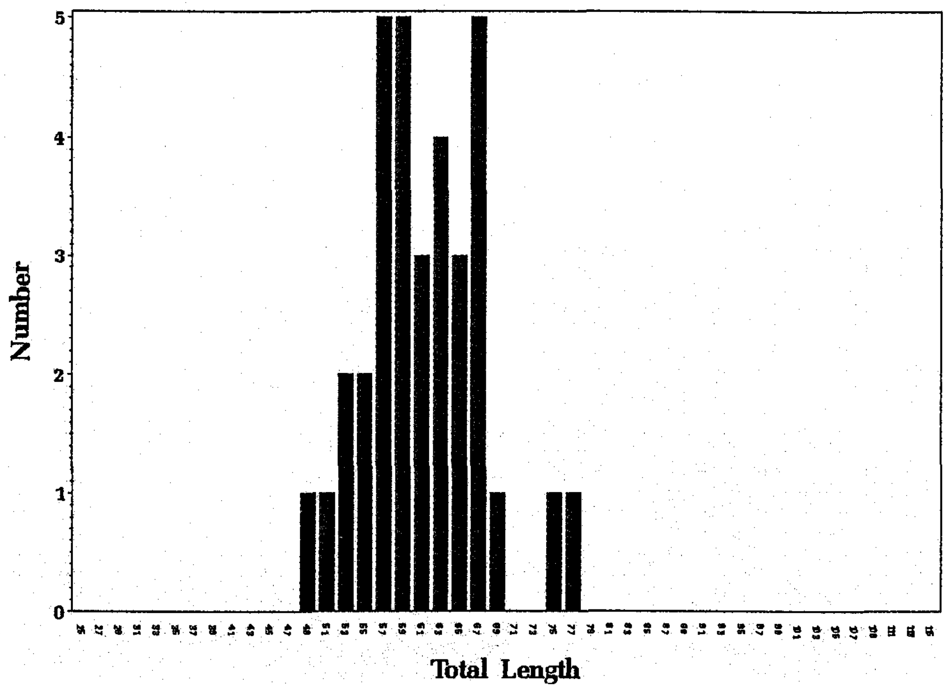
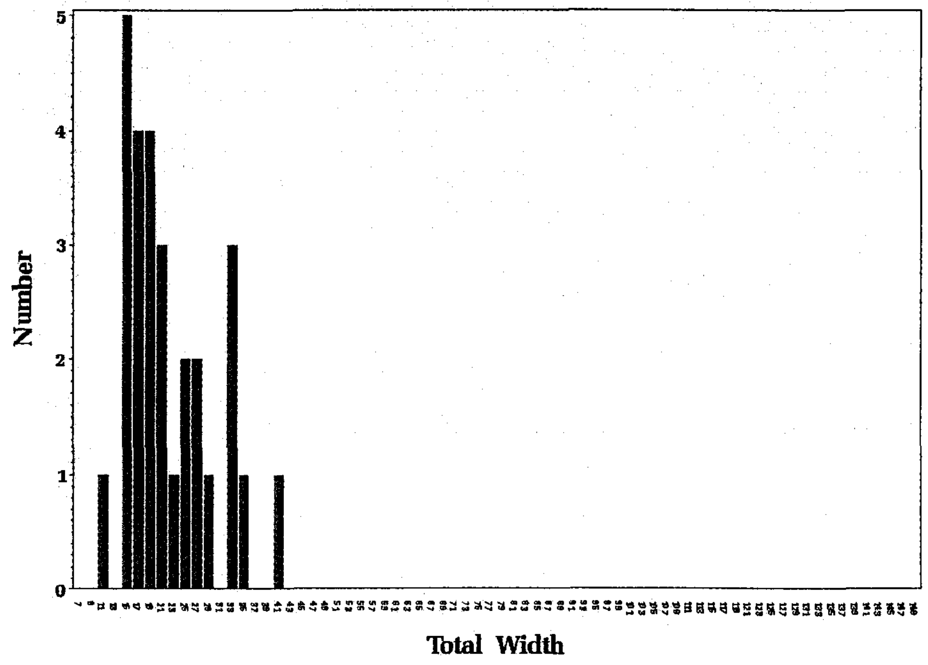
42501
51201
52501
61201
71001
72501
82801
91801
92501
100901
103001
111901
Date
Number
Biomass

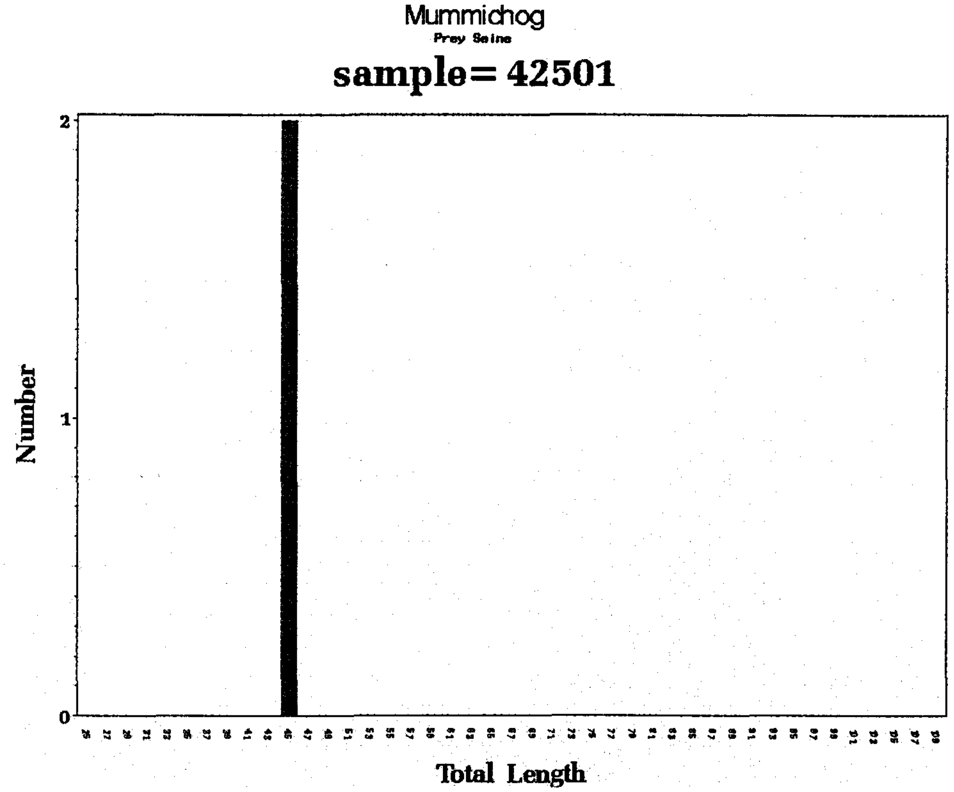
Appendix 3: This appendix contains the size distributions of the six most abundant species sampled with prey seine during the study. They are presented in order decreasing abundance specific to each sample date.

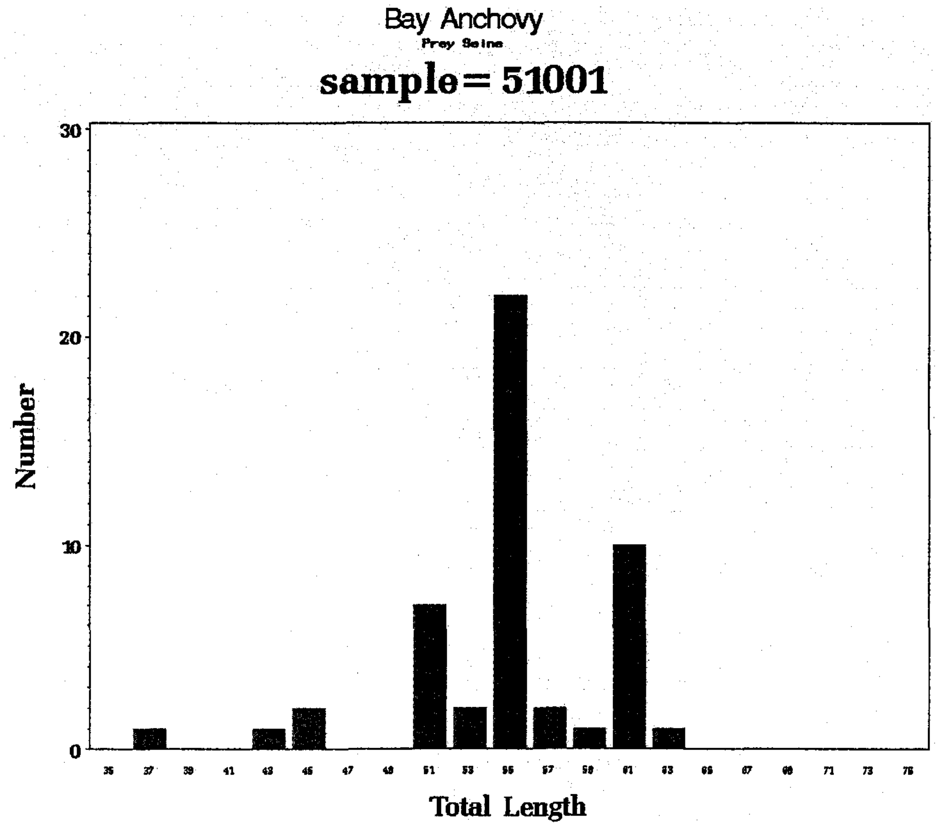


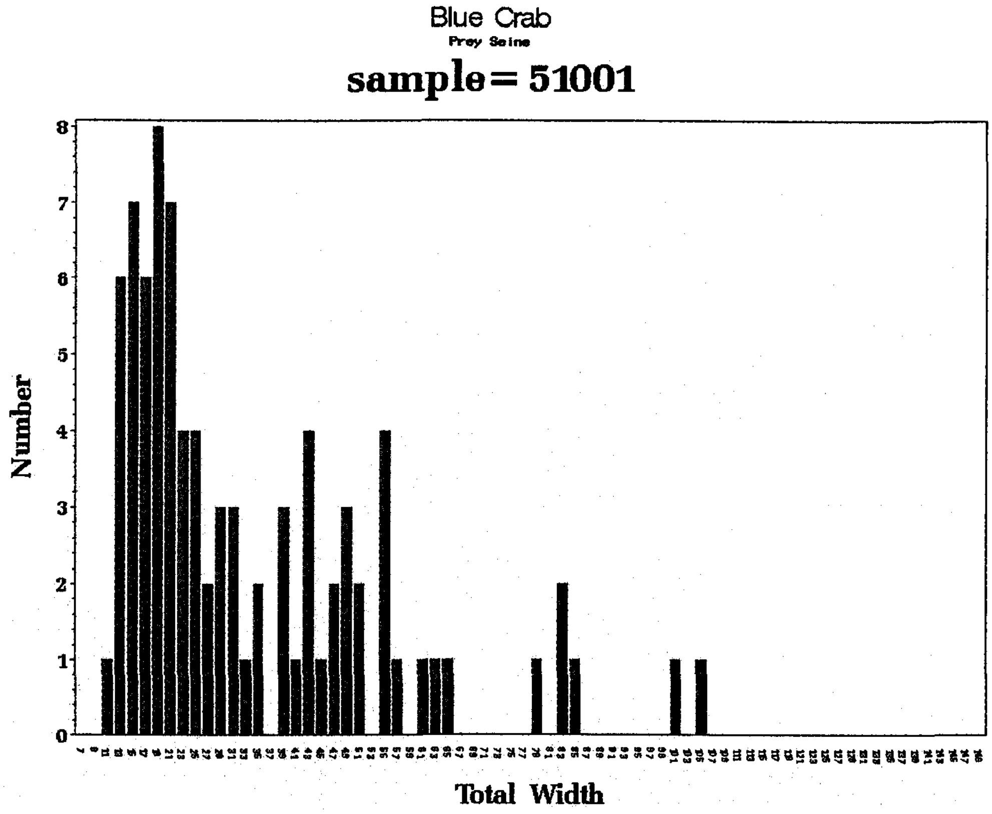
Striped Killifish
Prey Seine
sample= 42501

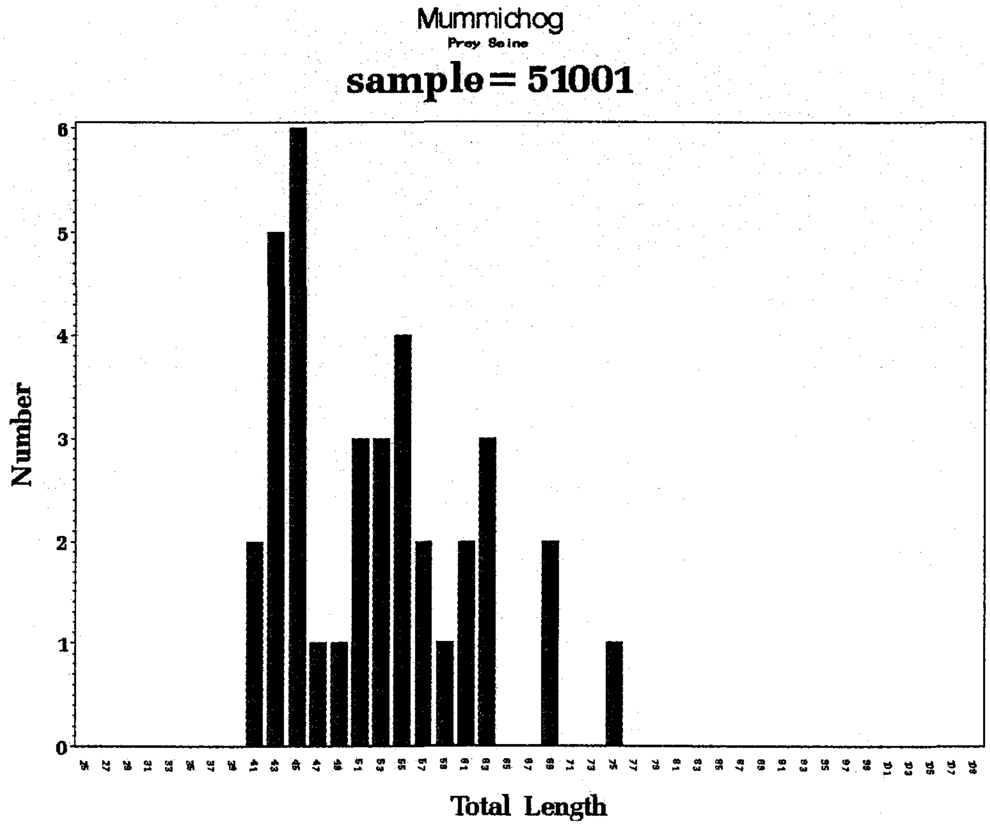


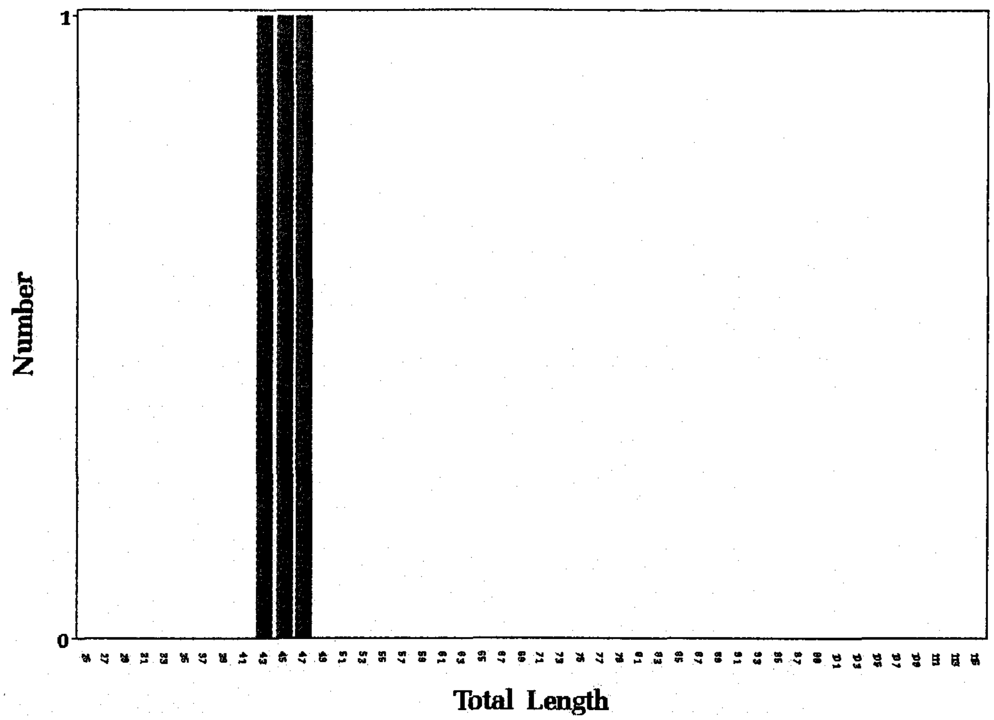
Blue Crab
Prey Seine
sample= 42501


Mummichog
Prey Seine
sample= 42501
Number
2
1
0
Total Length

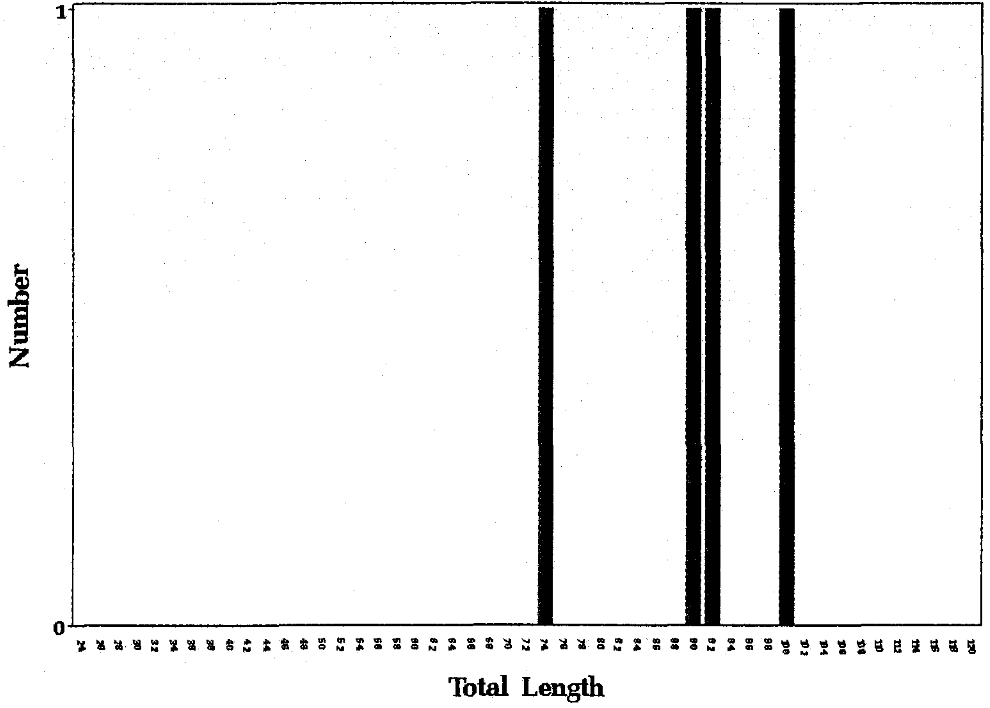

Bay Anchovy
Prey Seine
sample= 51001
Number
30
20
10
0
35
37
39
41
43
45
47
49
51
53
55
57
59
61
63
65
67
69
71
73
75
Total Length


Blue Crab
Prey Seine
sample= 51001
Number
0
1
2
3
4
5
6
7
8
Total Width


Mummichog
Prey Seine
sample= 51001
Number
0
1
2
3
4
5
6
Total Length

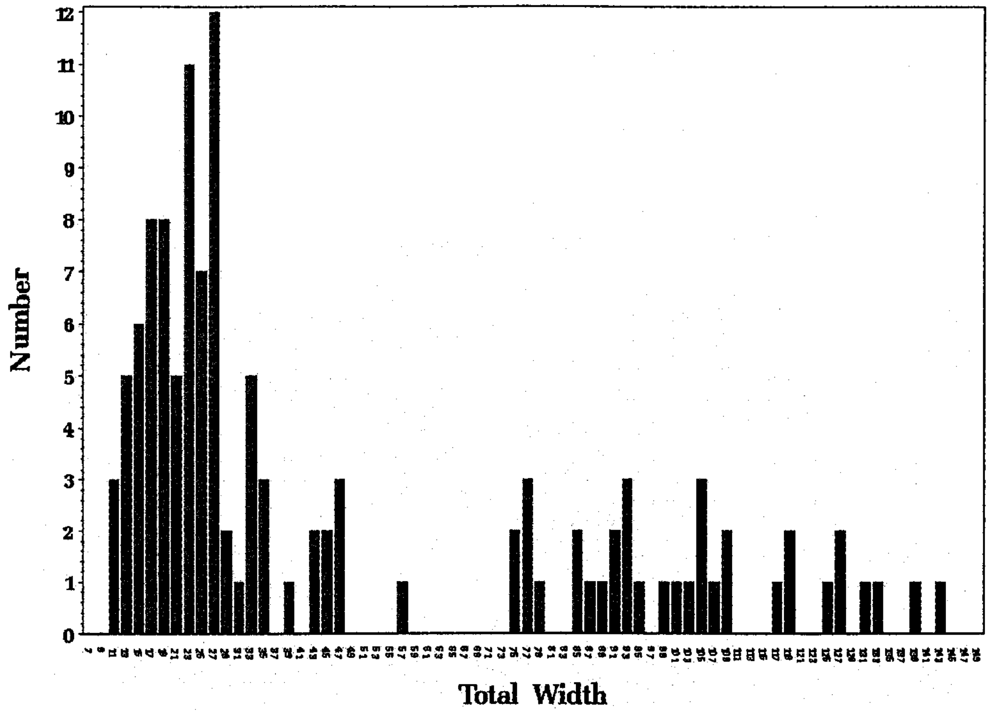


Striped Killifish
Prey Seine
sample= 51001

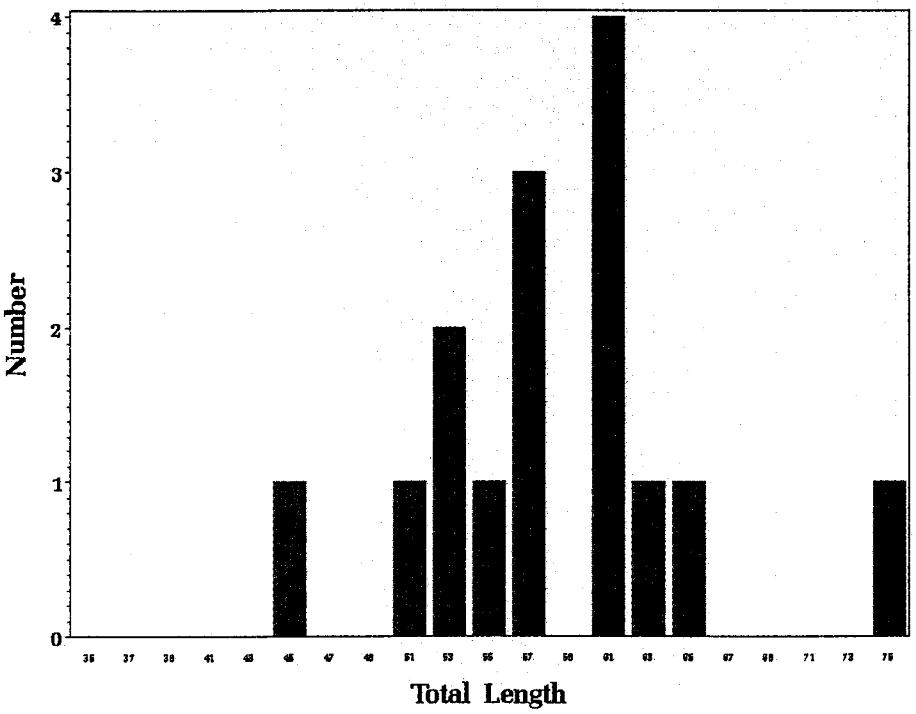


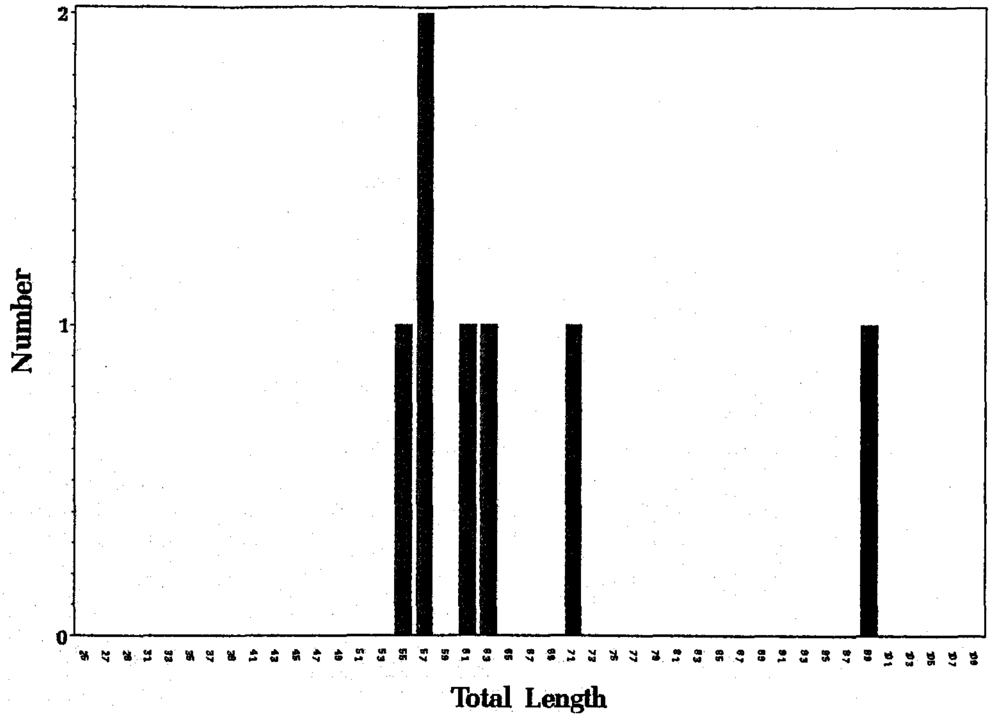
Atlantic Silverside
Prey Seine
sample= 51001

Blue Crab
Prey Seine
sample= 52501



Bay Anchovy
Prey Seine
sample= 52501

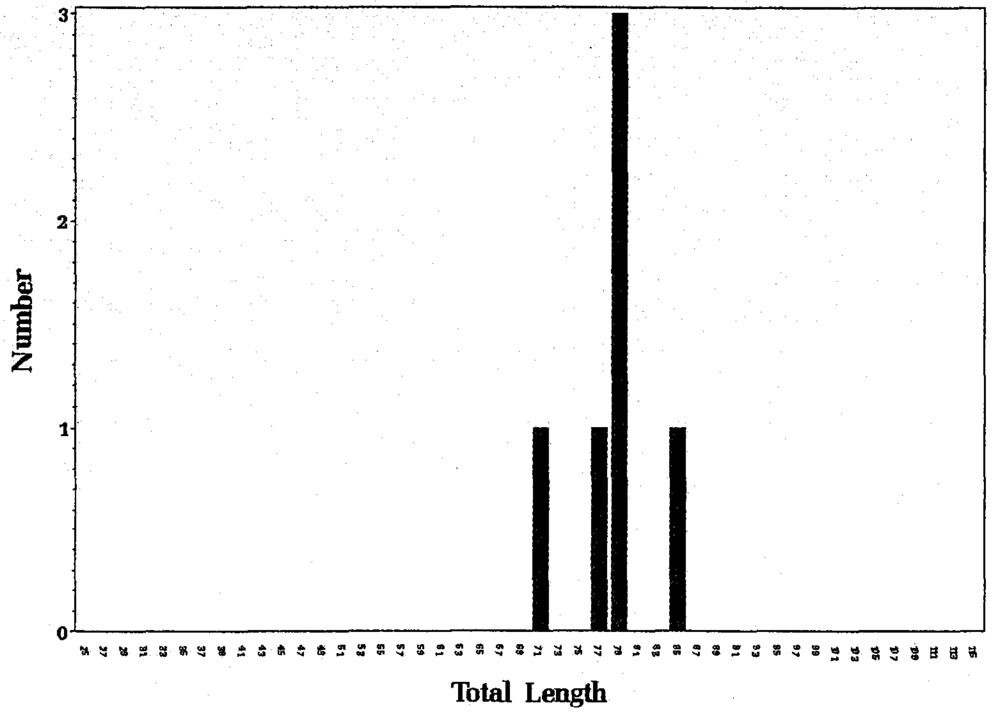




Mummichog

Prey Seine

sample= 52501



Striped Killifish

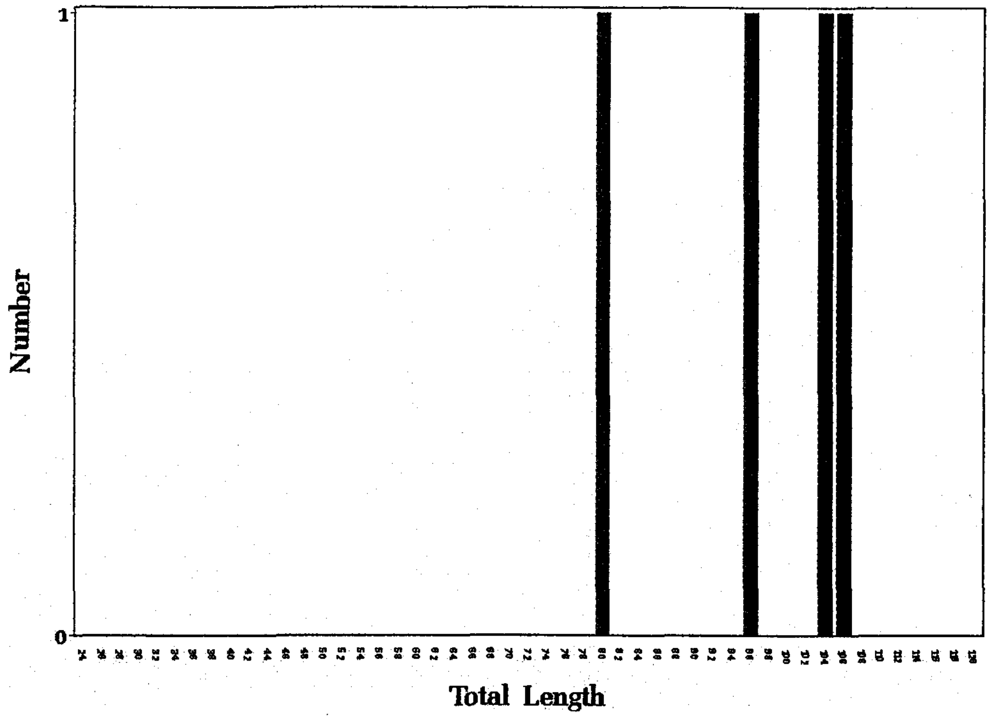
Prey Seine

sample= 52501

Atlantic Silverside

Prey Seine

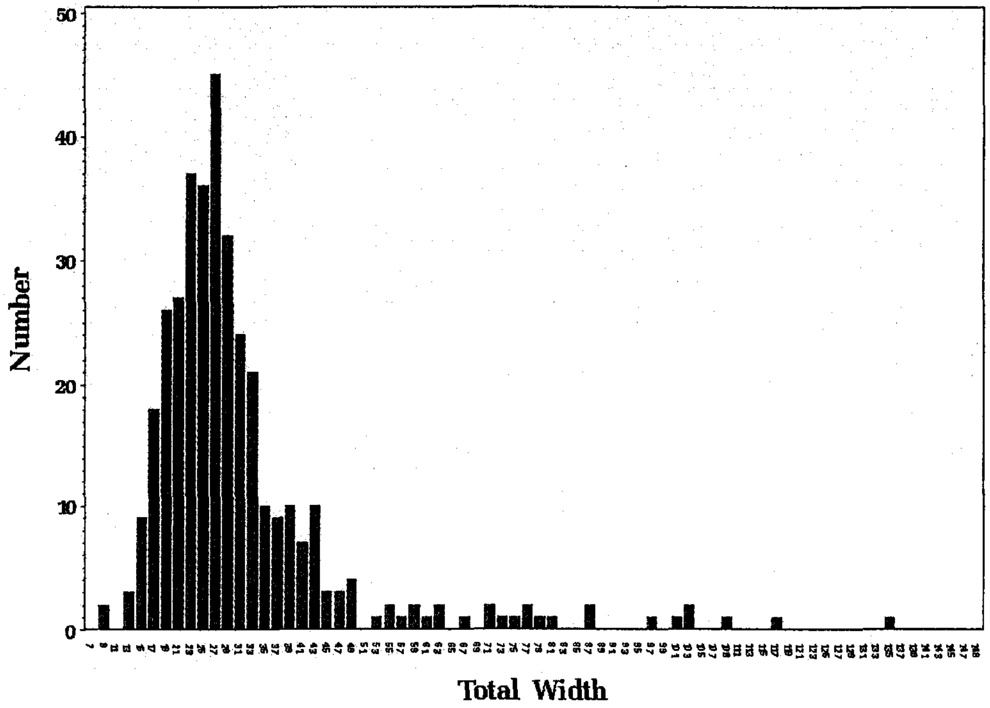
sample= 52501



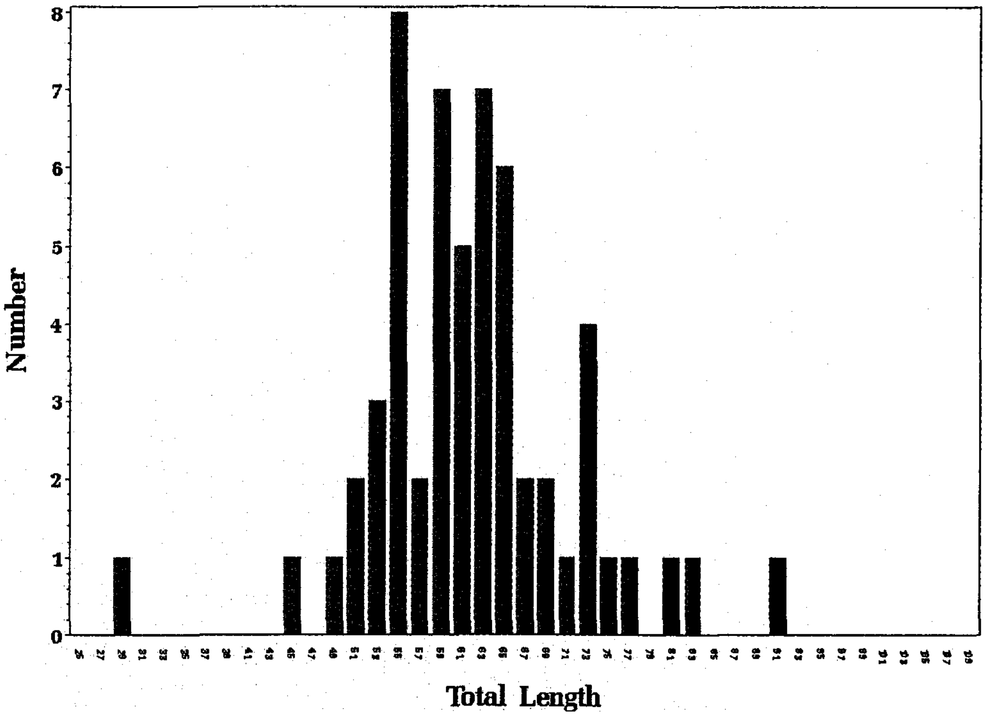
Blue Crab

Prey Seine

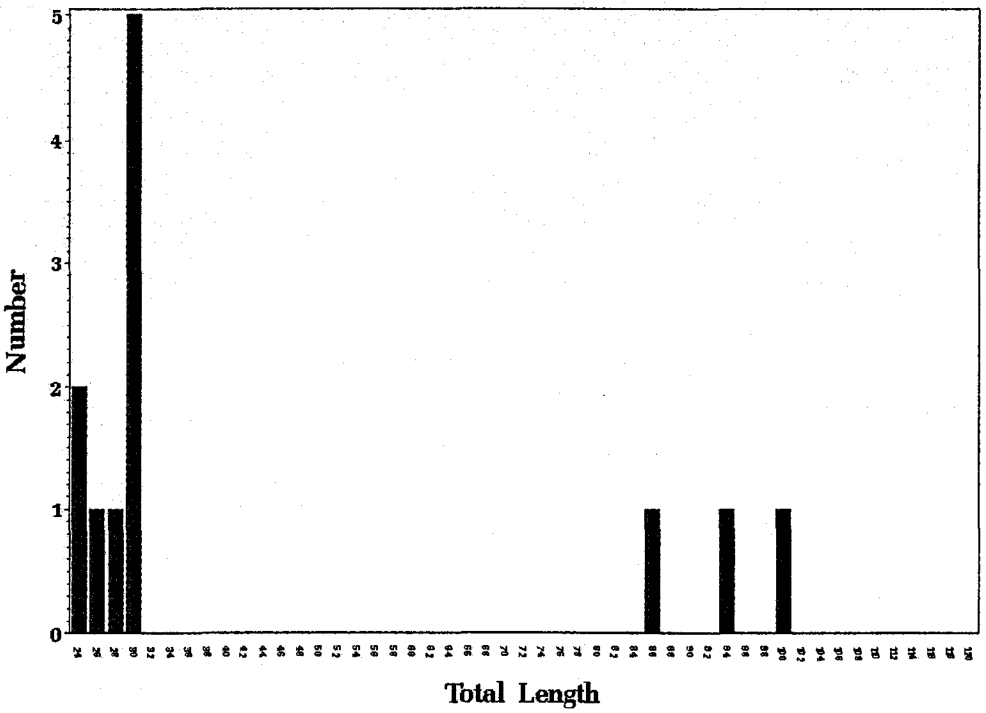
sample= 61201

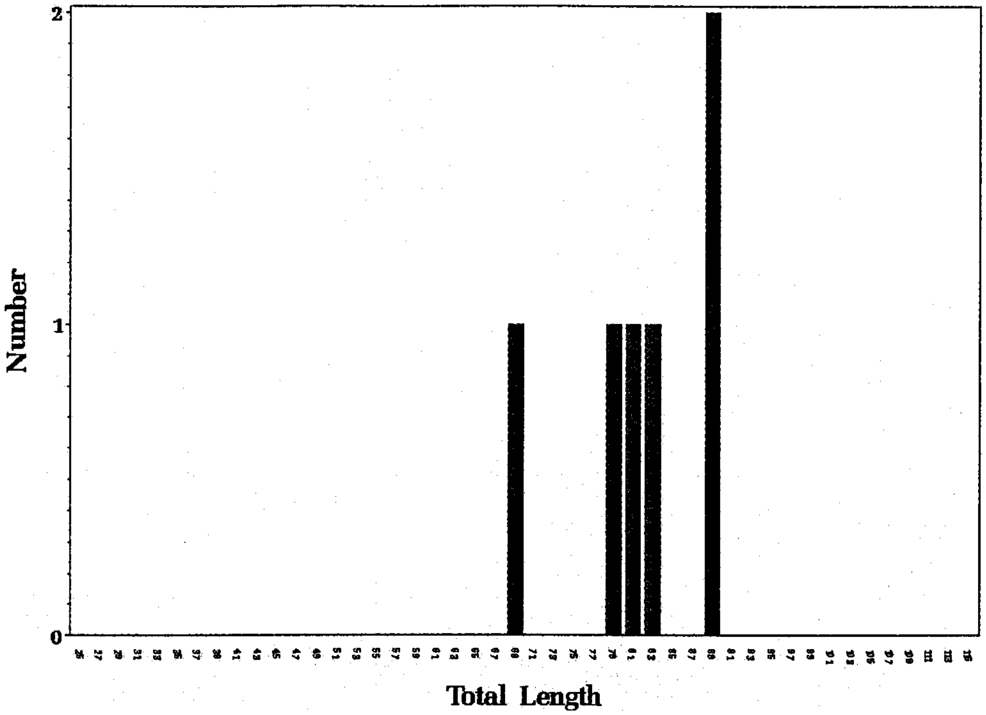


Mummichog
Prey Seine
sample= 61201

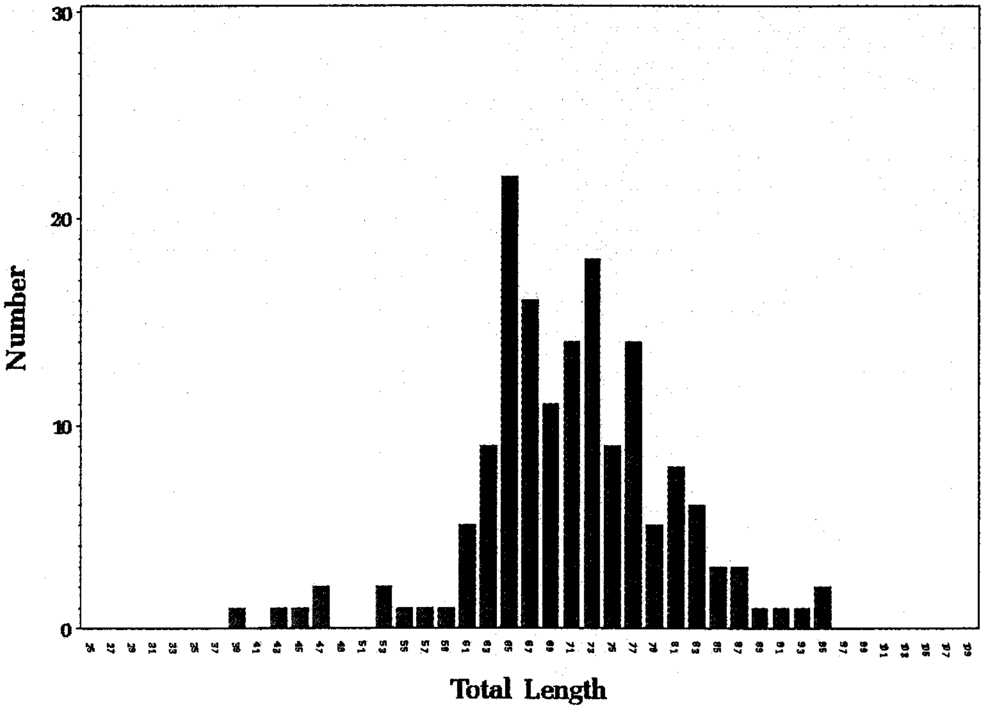


Atlantic Silverside
Prey Seine
sample= 61201





Striped Killifish
Prey Seine
sample= 61201

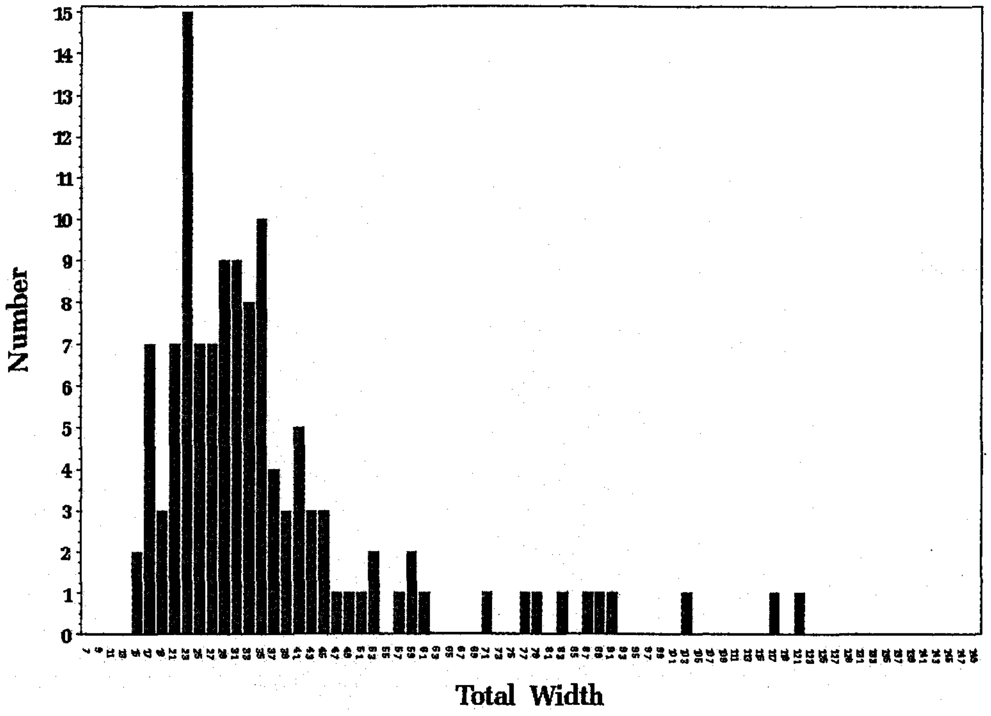


Mummichog
Prey Seine
sample= 71001

Blue Crab

Prey Seine

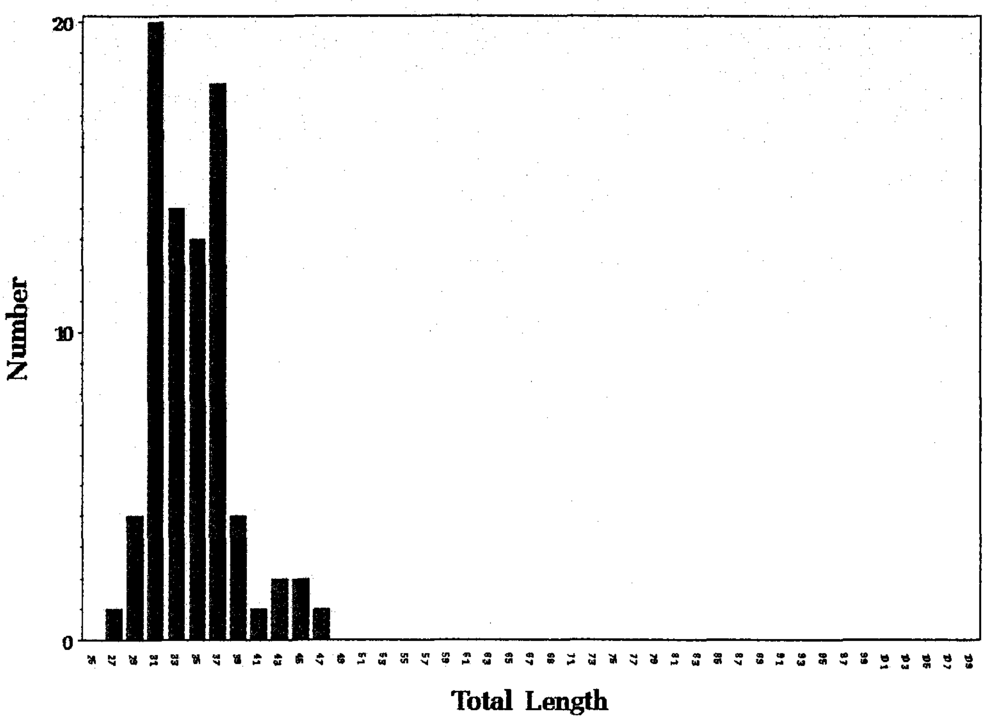
sample= 71001

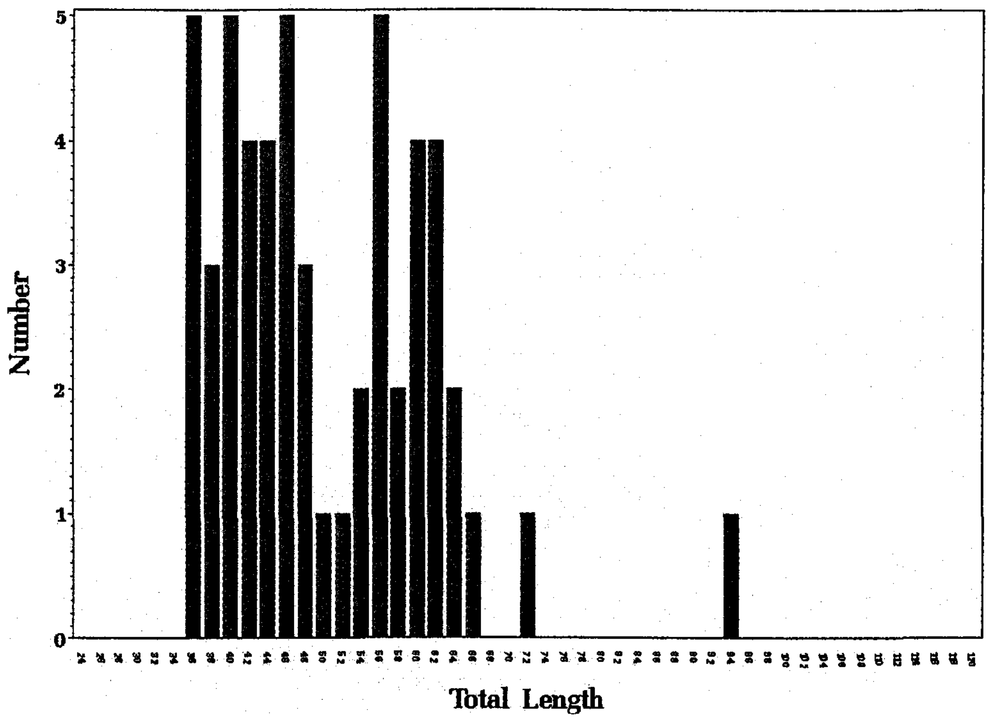


Silver Perch

Prey Seine

sample= 71001

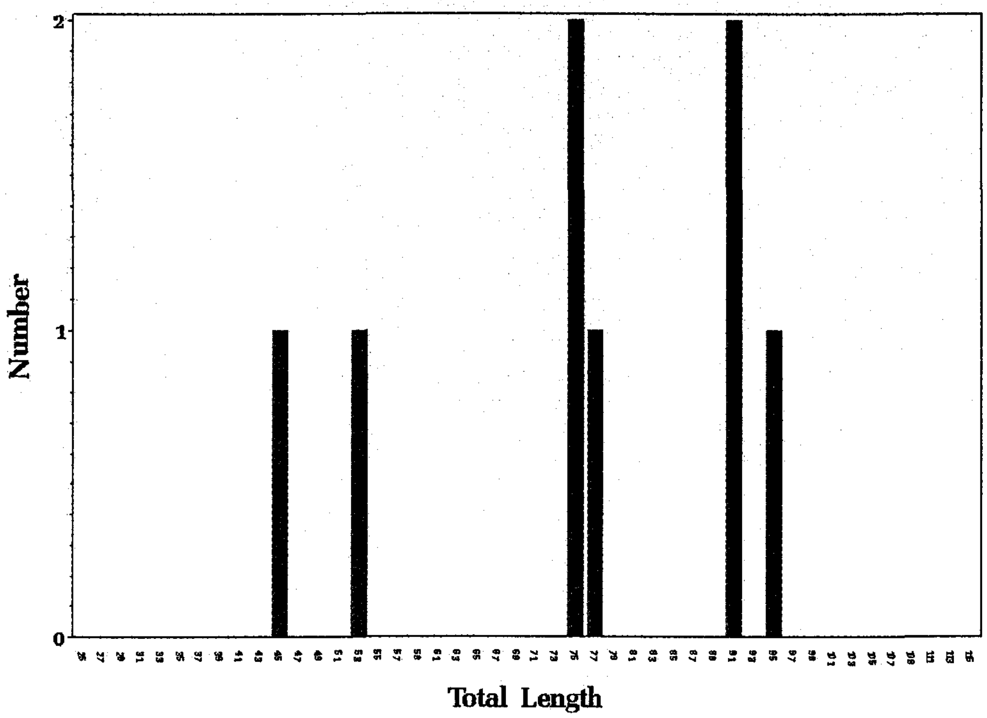




Atlantic Silverside

Prey Seine

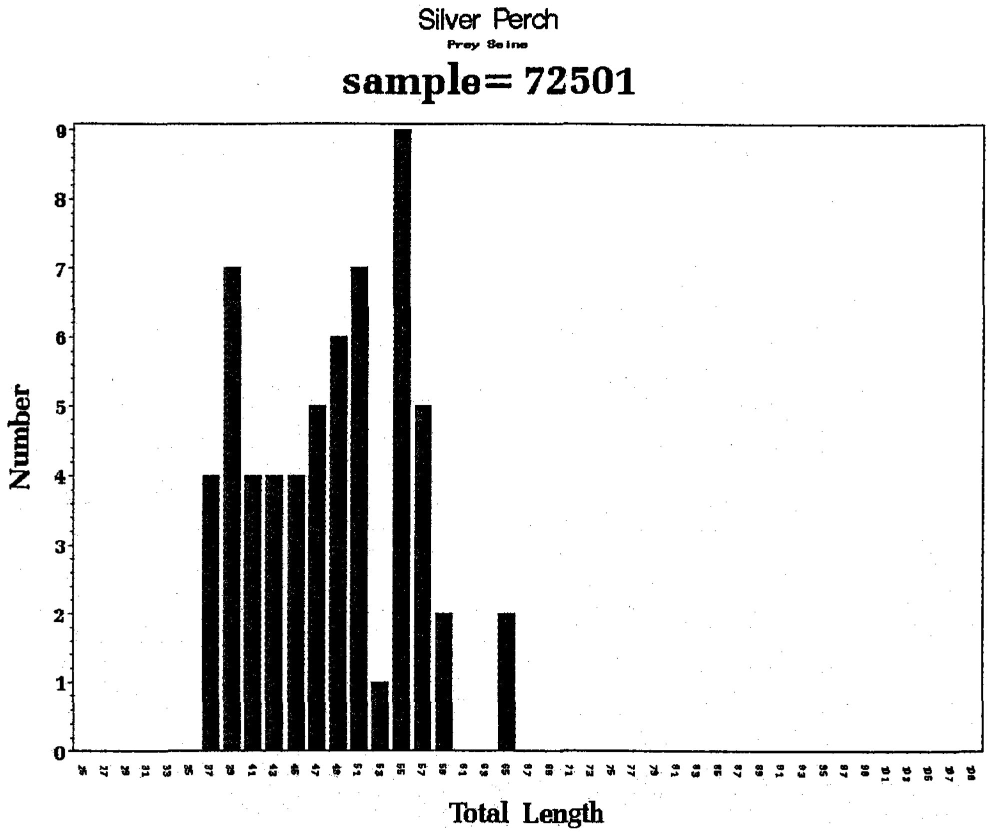
sample= 71001



Striped Killifish

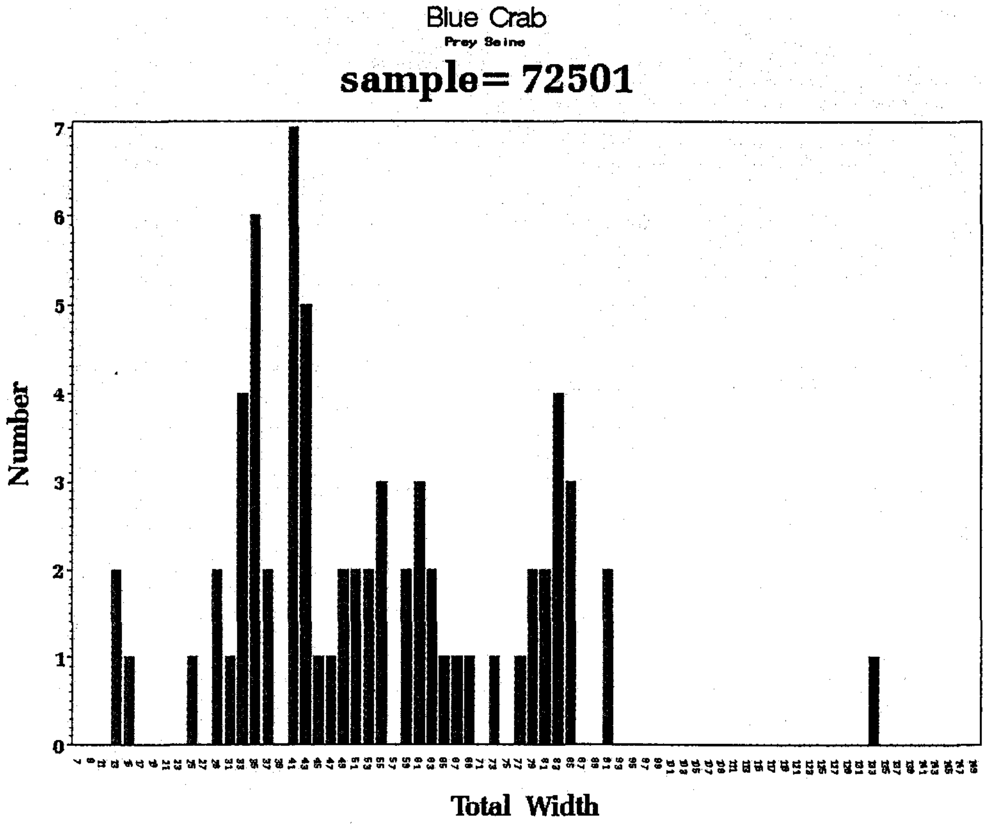
Prey Seine

sample= 71001


Silver Perch

Prey Seine

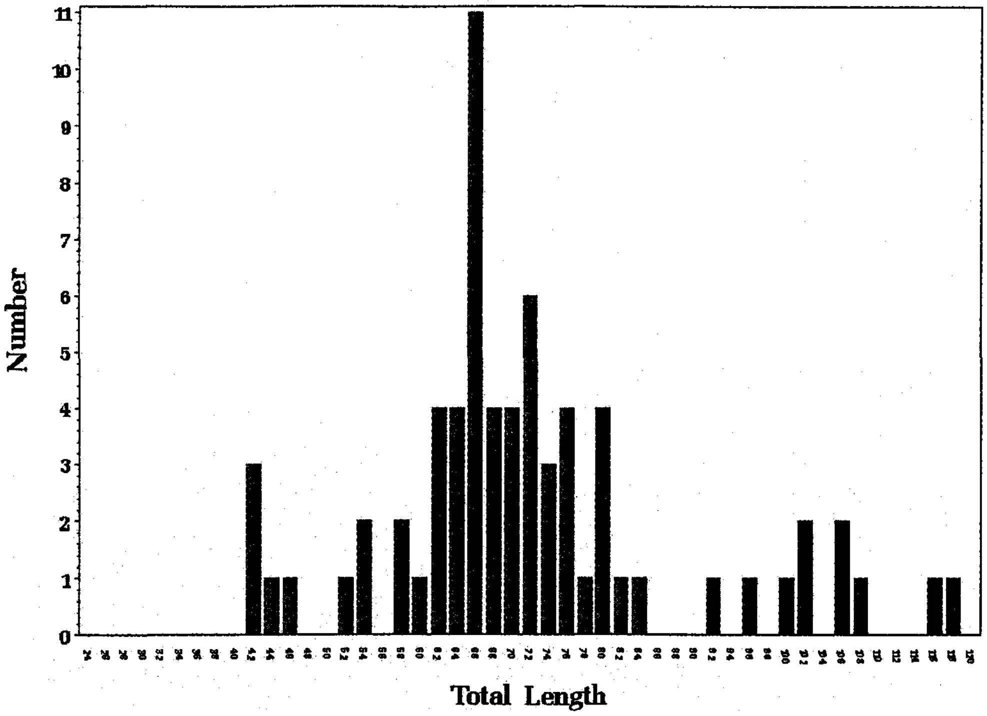
sample= 72501


Blue Crab

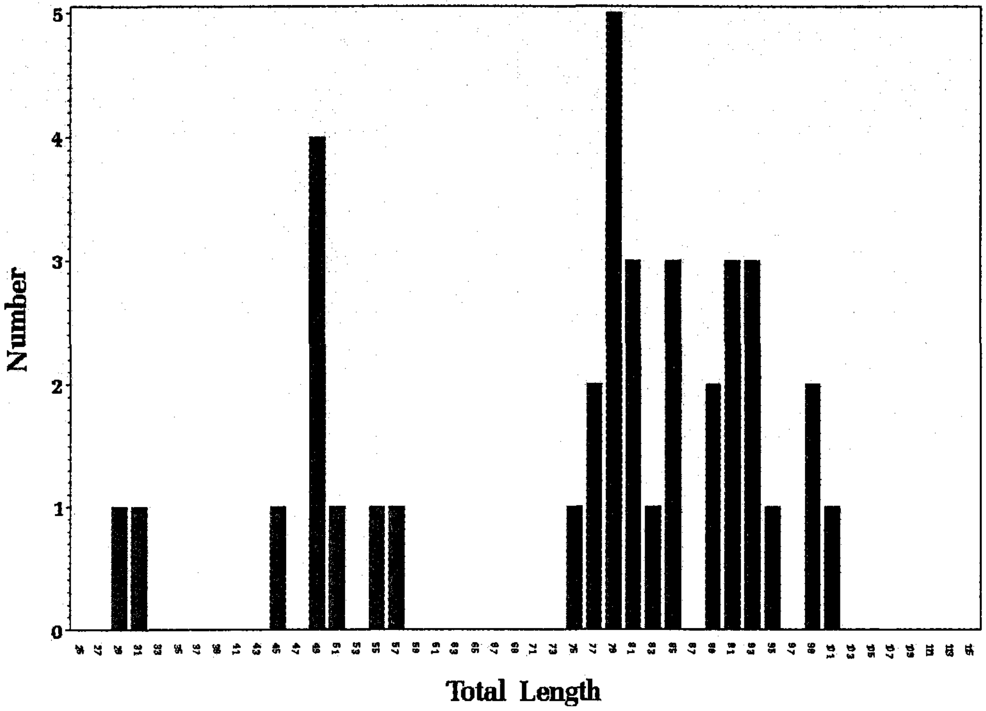
Prey Seine

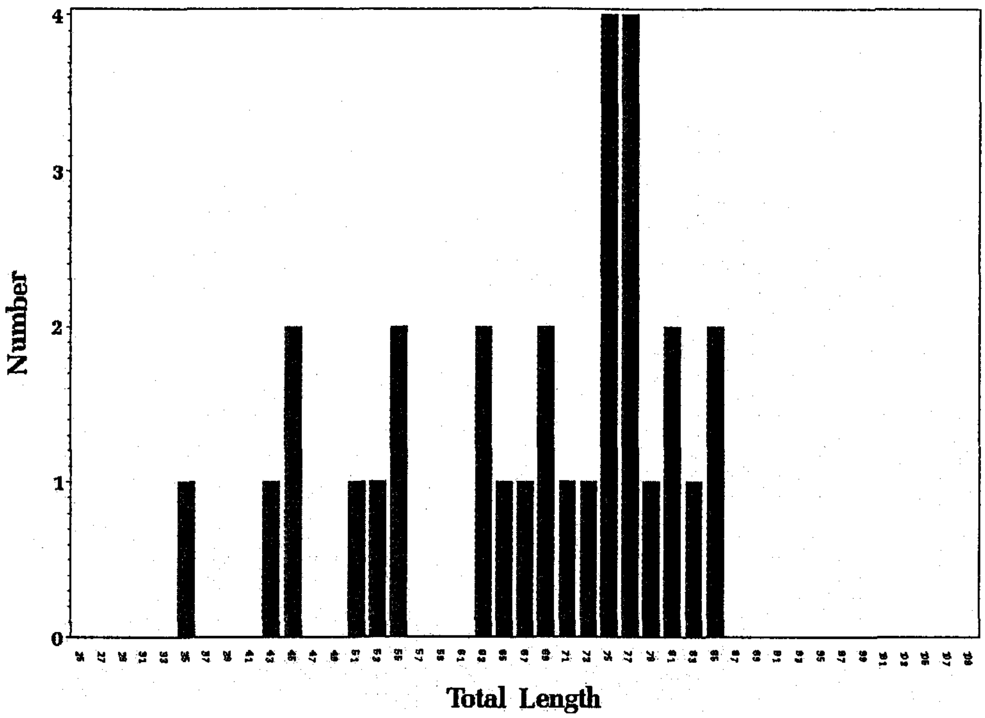
sample= 72501

Atlantic Silverside
Prey Seine
sample= 72501



Striped Killifish
Prey Seine
sample= 72501

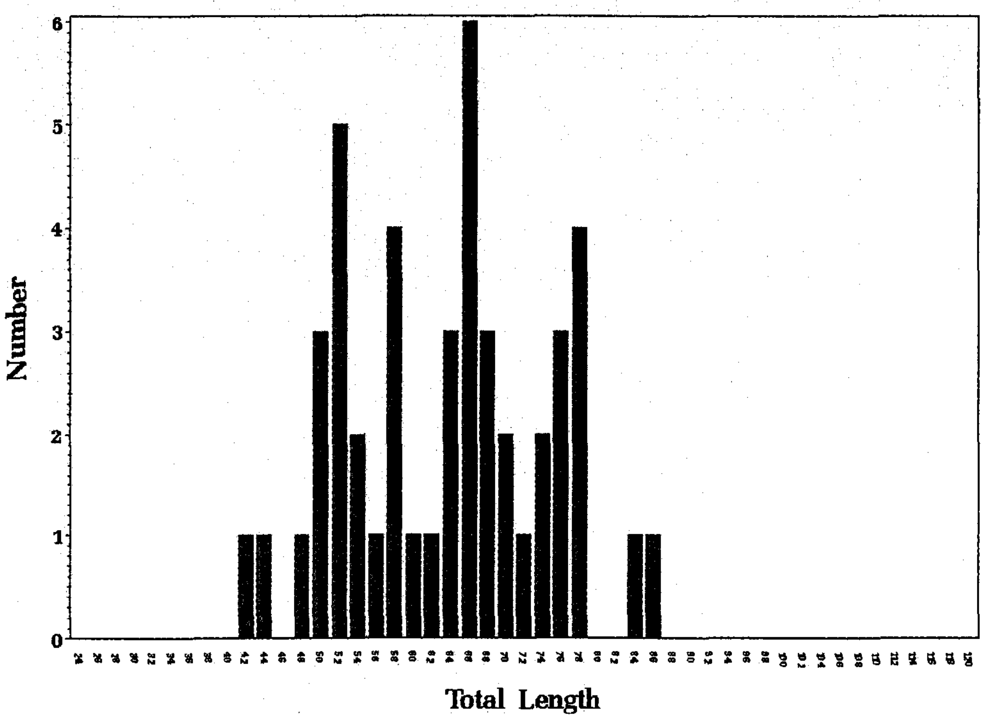




Mummichog

Prey Seine

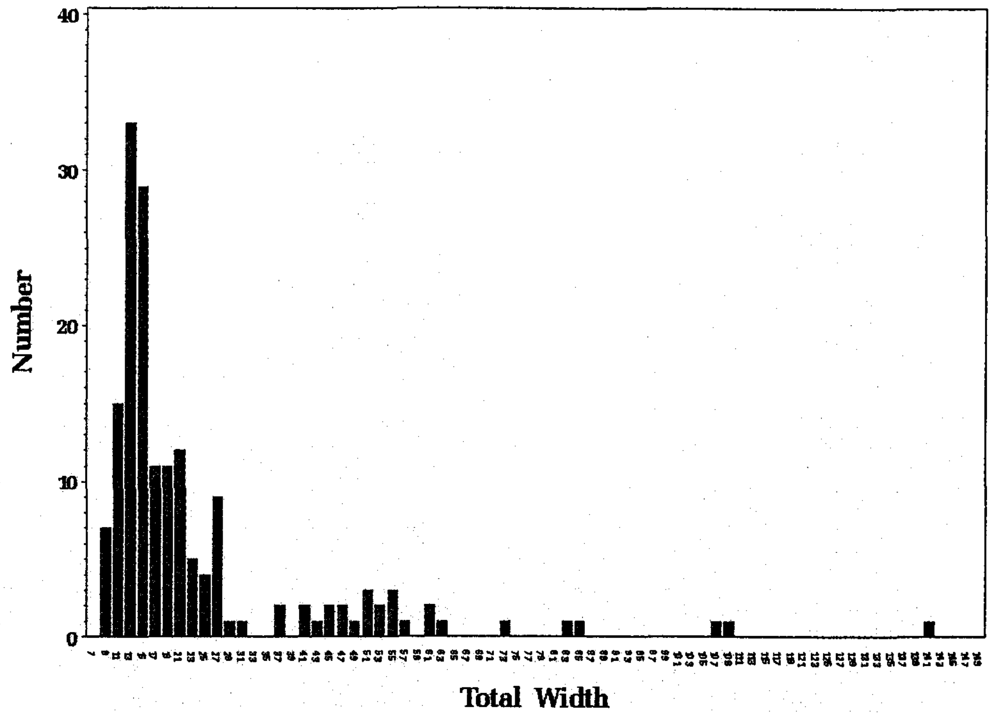
sample= 72501



Atlantic Silverside

Prey Seine

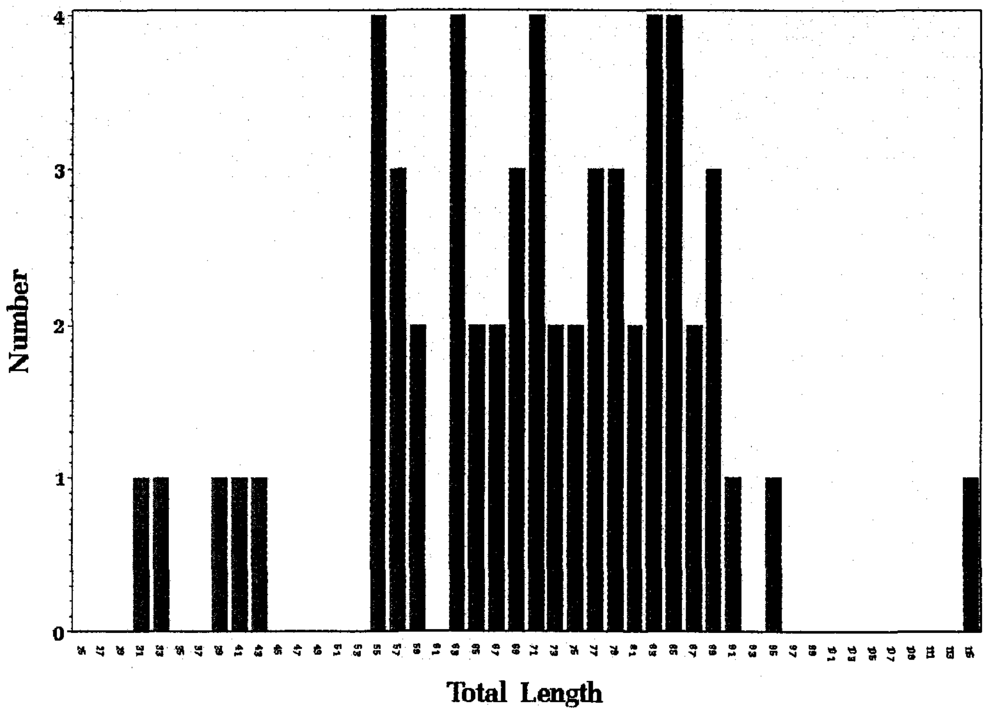
sample= 82801



Blue Crab

Prey Seine

sample= 82801



Striped Killifish

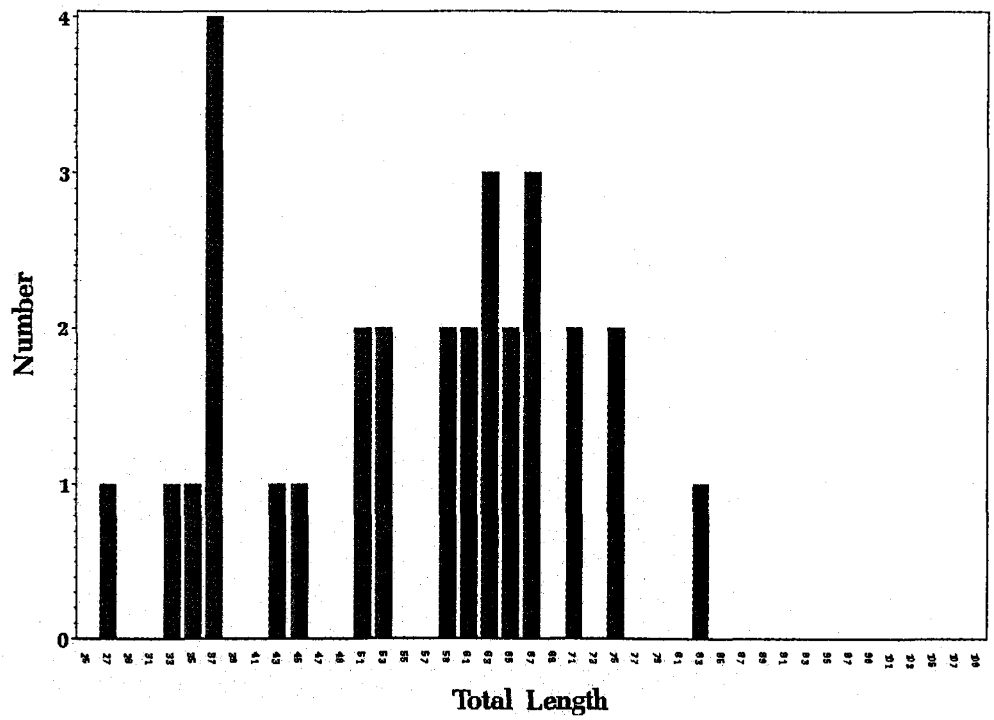
Prey Seine

sample= 82801

Silver Perch

Prey Seine

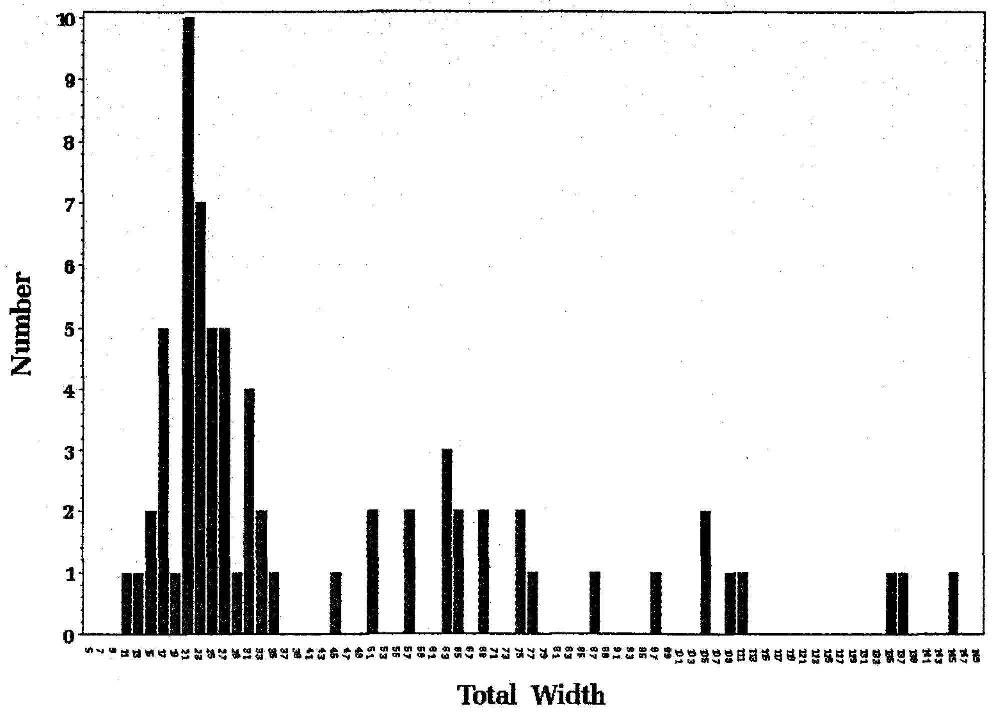
sample= 82801

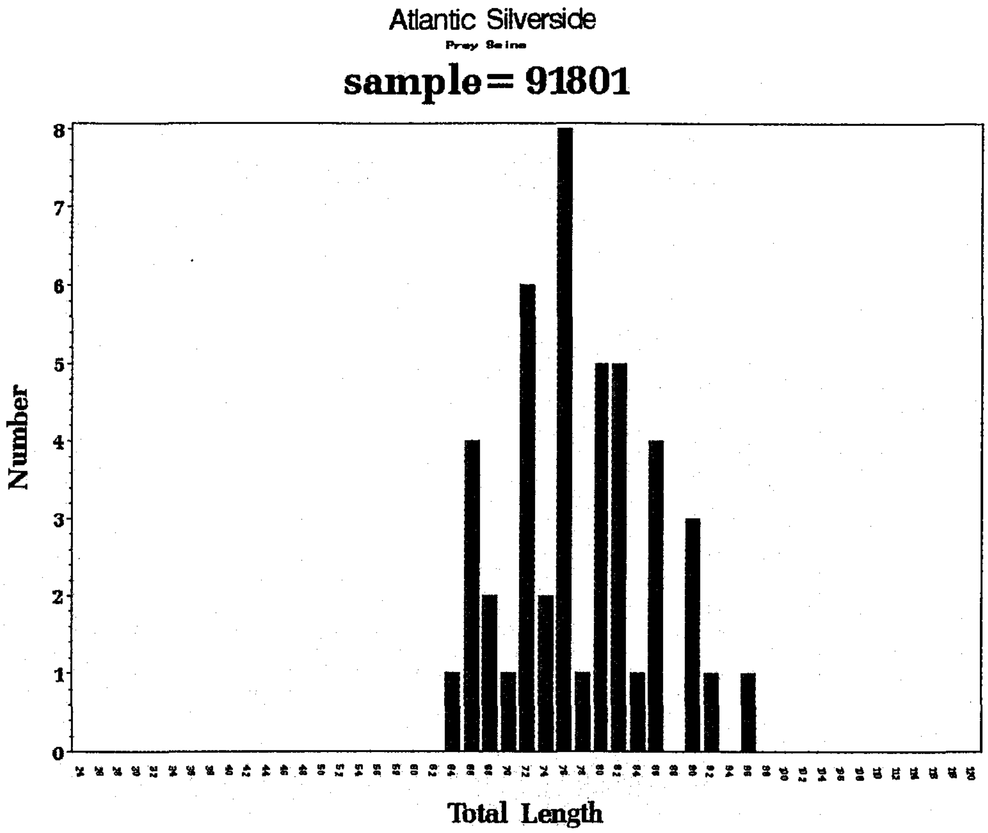


Blue Crab

Prey Seine

sample= 91801

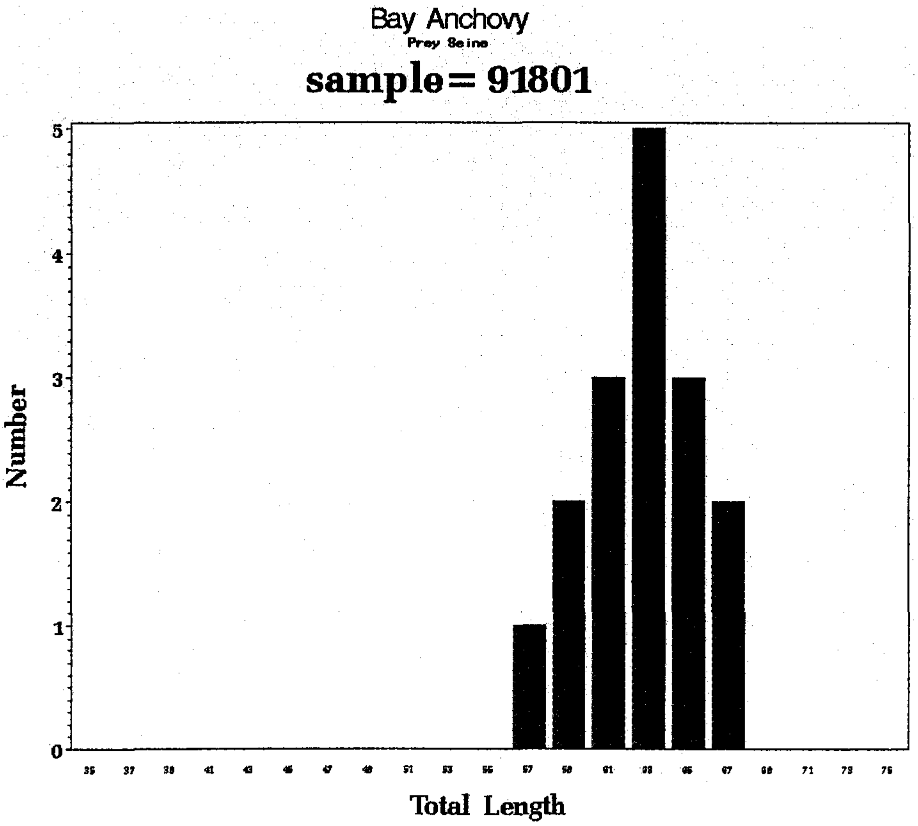




Atlantic Silverside

Prey Seine

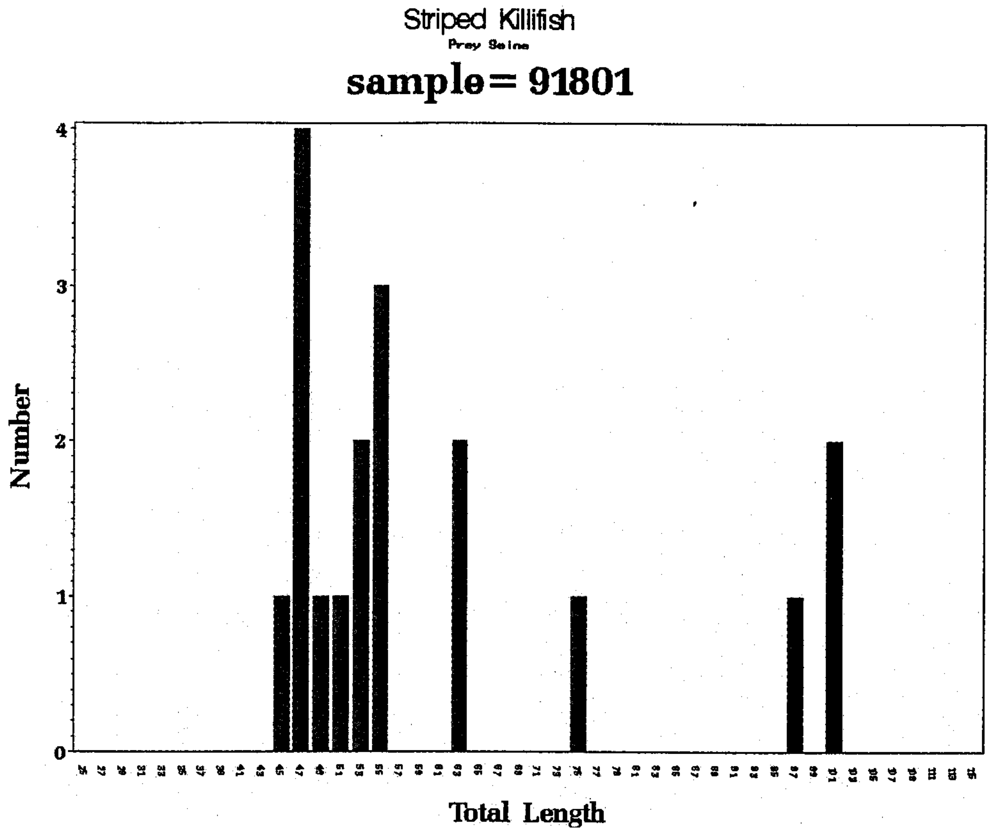
sample= 91801

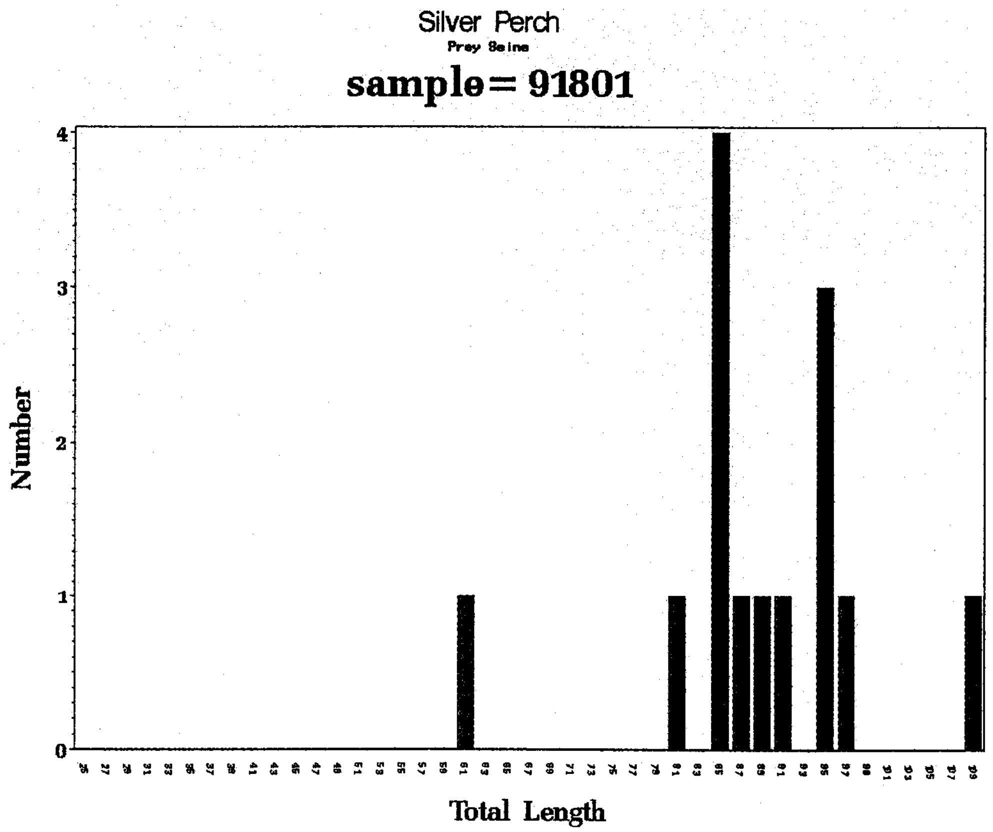


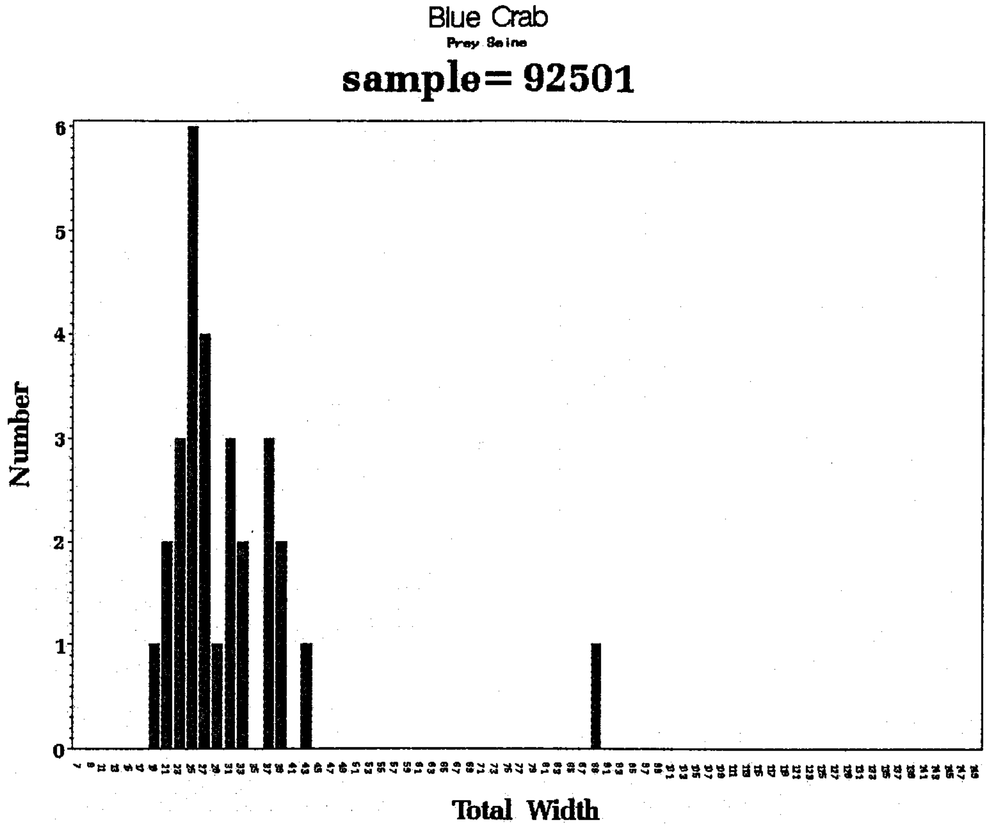
Bay Anchovy

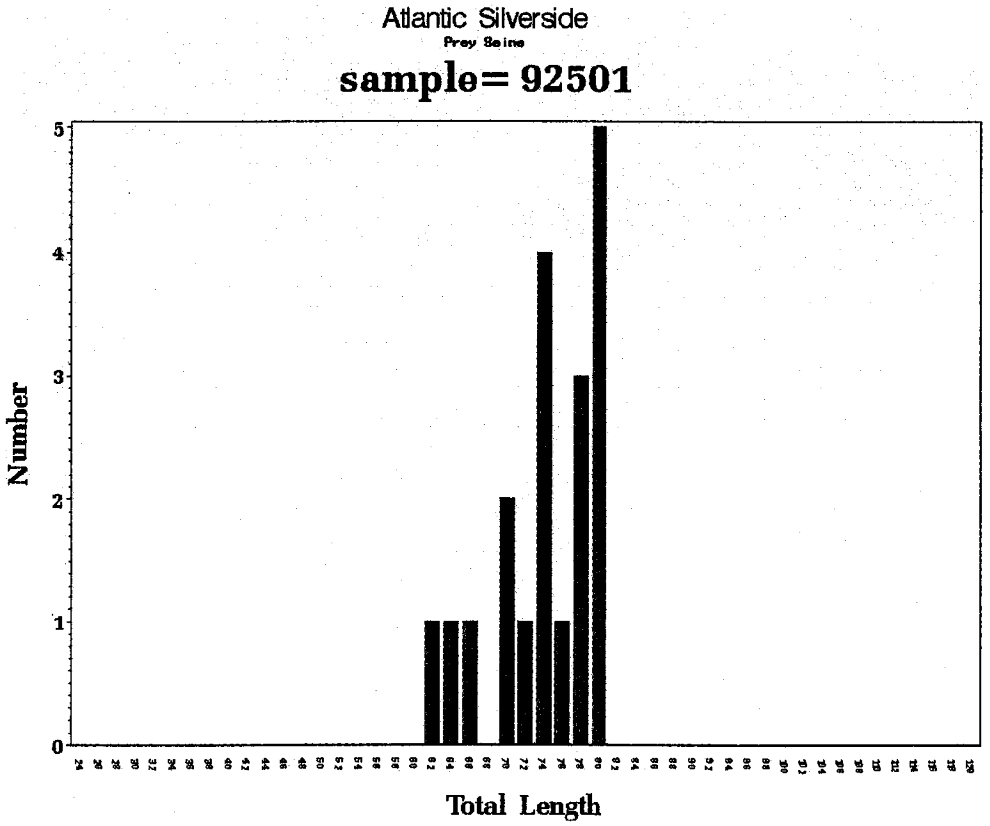
Prey Seine

sample= 91801

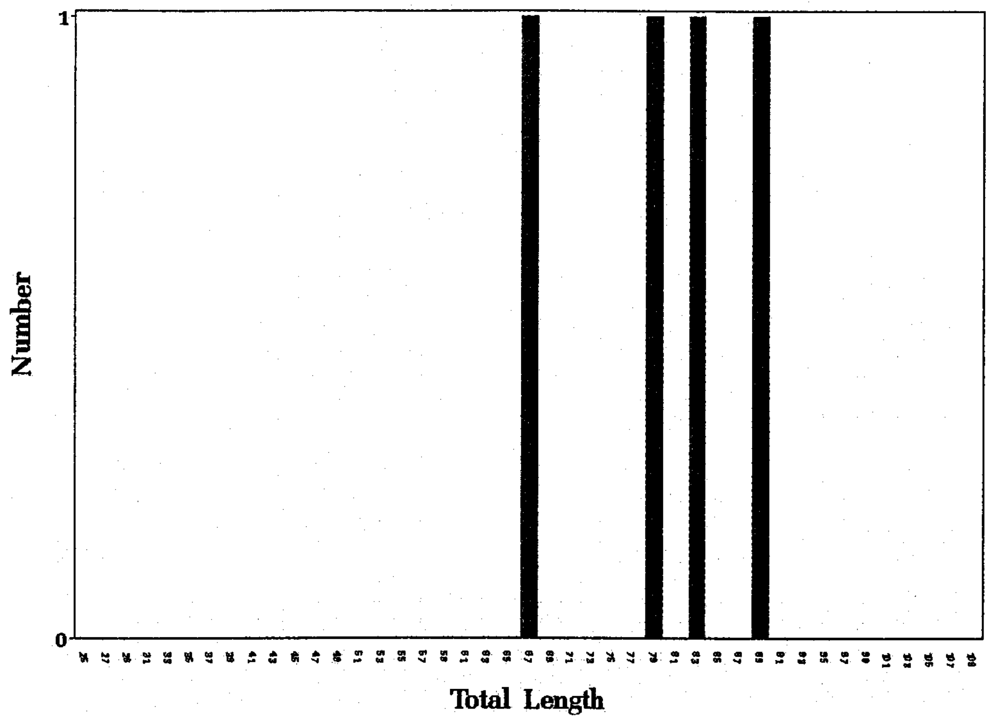

Striped Killifish
Prey Seine
sample= 91801
Number
0
1
2
3
4
Total Length


Silver Perch
Prey Seine
sample= 91801
Number
0
1
2
3
4
Total Length

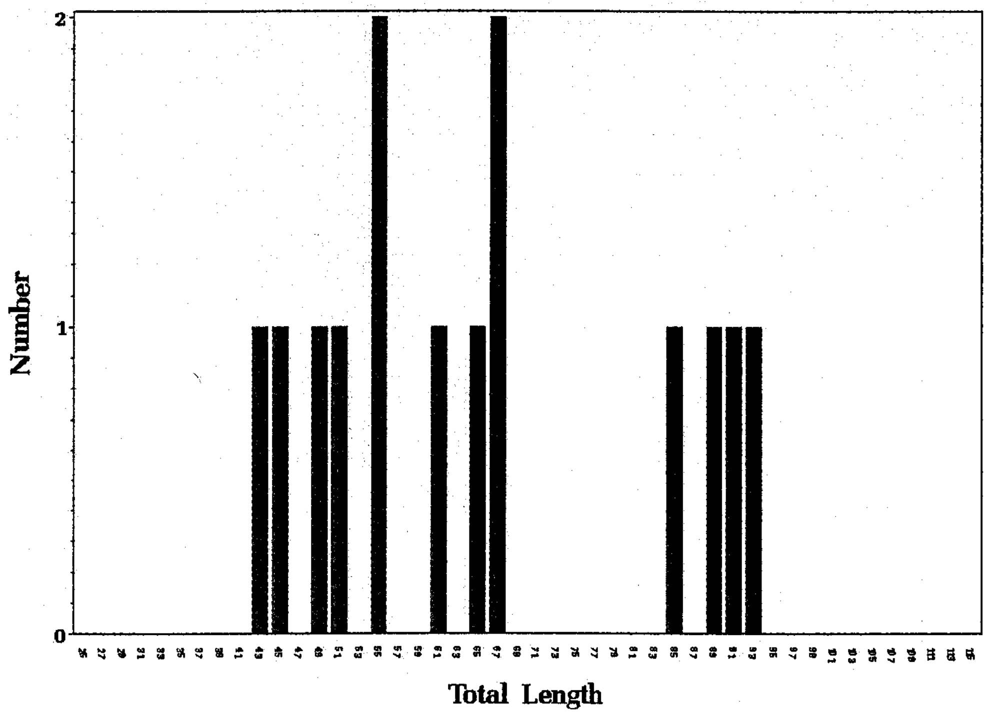

Blue Crab
Prey Seine
sample= 92501
Number
0
1
2
3
4
5
6
Total Width

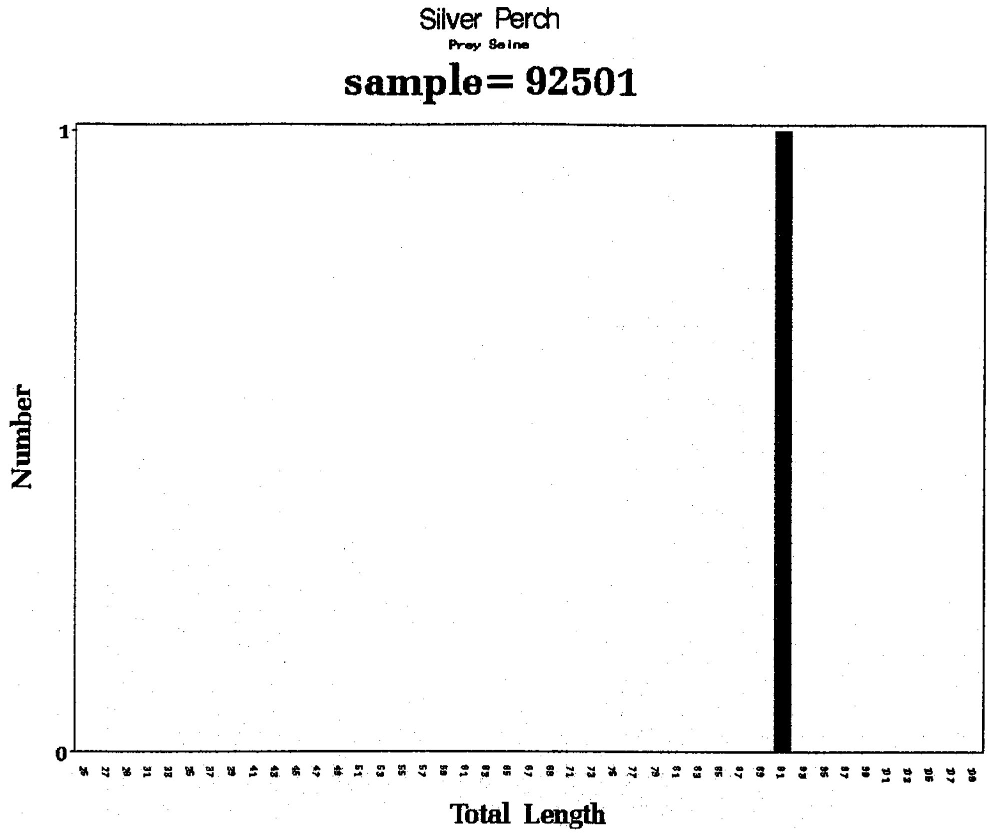

Atlantic Silverside
Prey Seine
sample= 92501
Number
0
1
2
3
4
5
Total Length

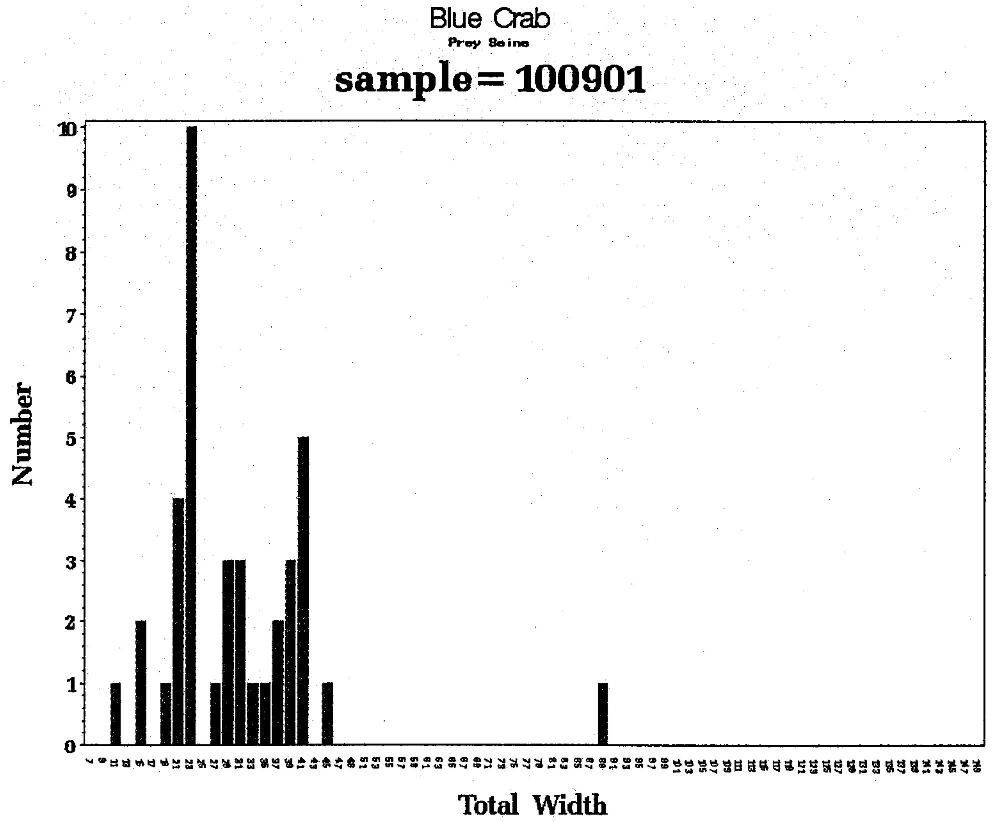
Mummichog
Prey Seine
sample= 92501



Striped Killifish
Prey Seine
sample= 92501



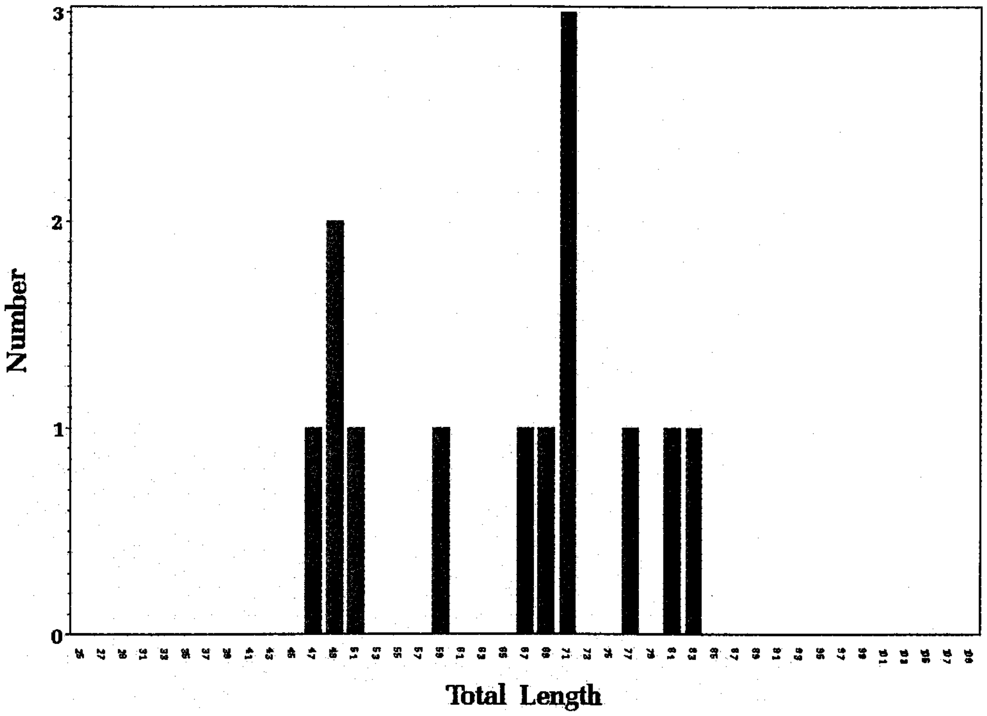

Silver Perch
Prey Seine
sample= 92501
Number
1
0
Total Length


Blue Crab
Prey Seine
sample= 100901
Number
10
9
8
7
6
5
4
3
2
1
0
Total Width

Mummichog

Prey Seine

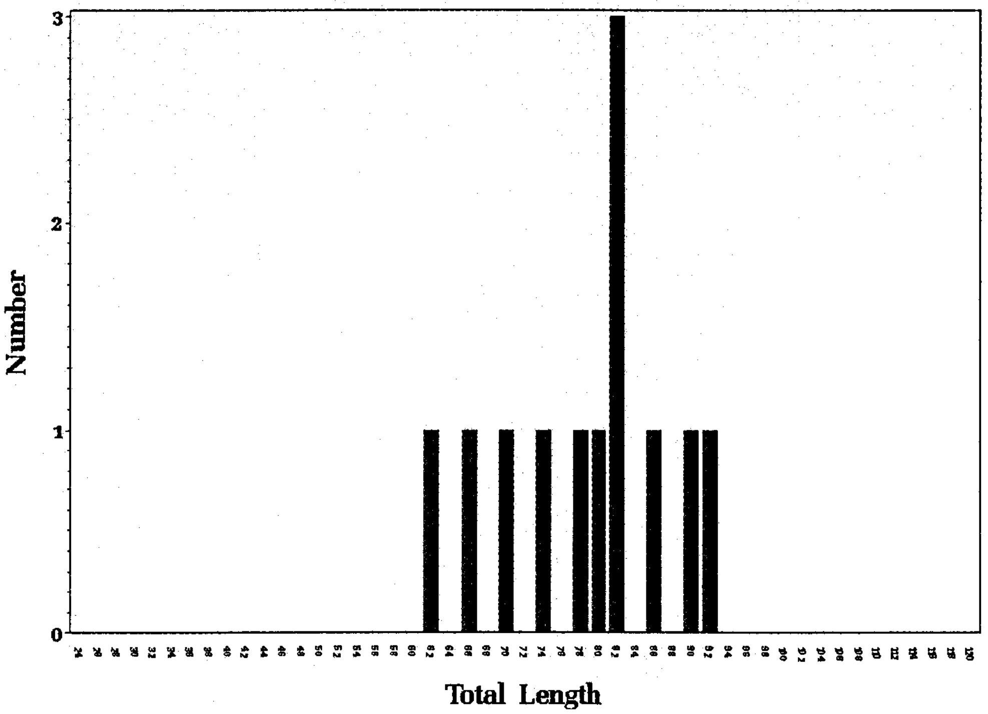
sample= 100901

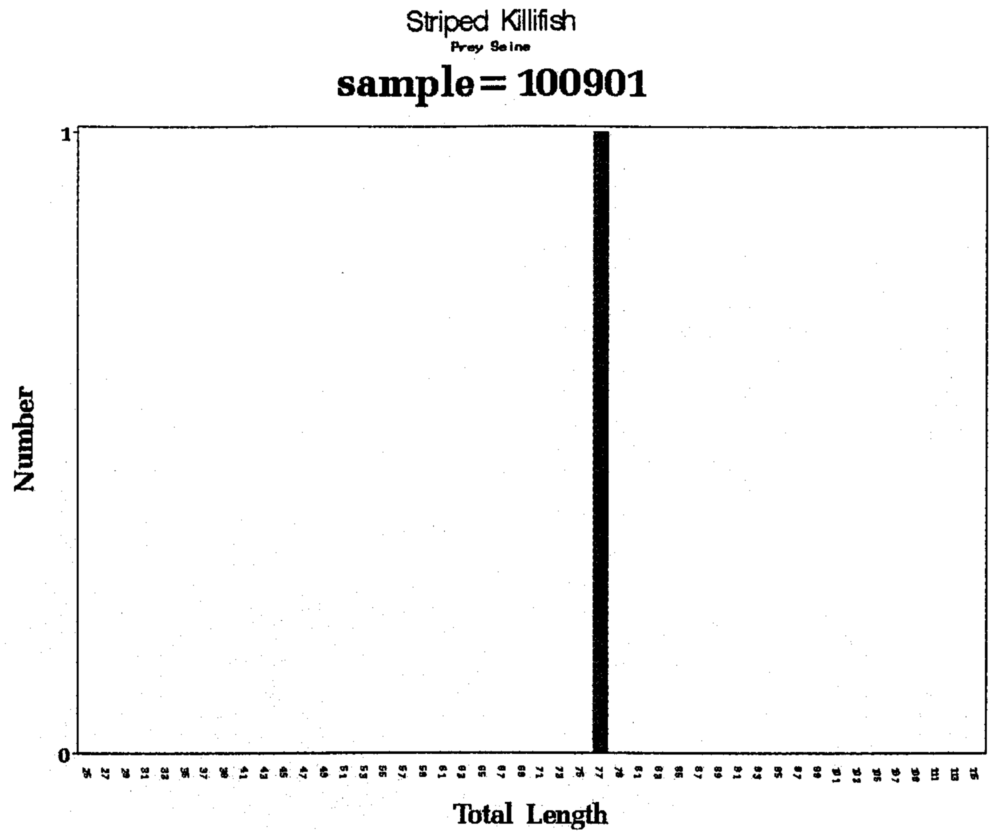


Atlantic Silverside

Prey seine

sample= 100901

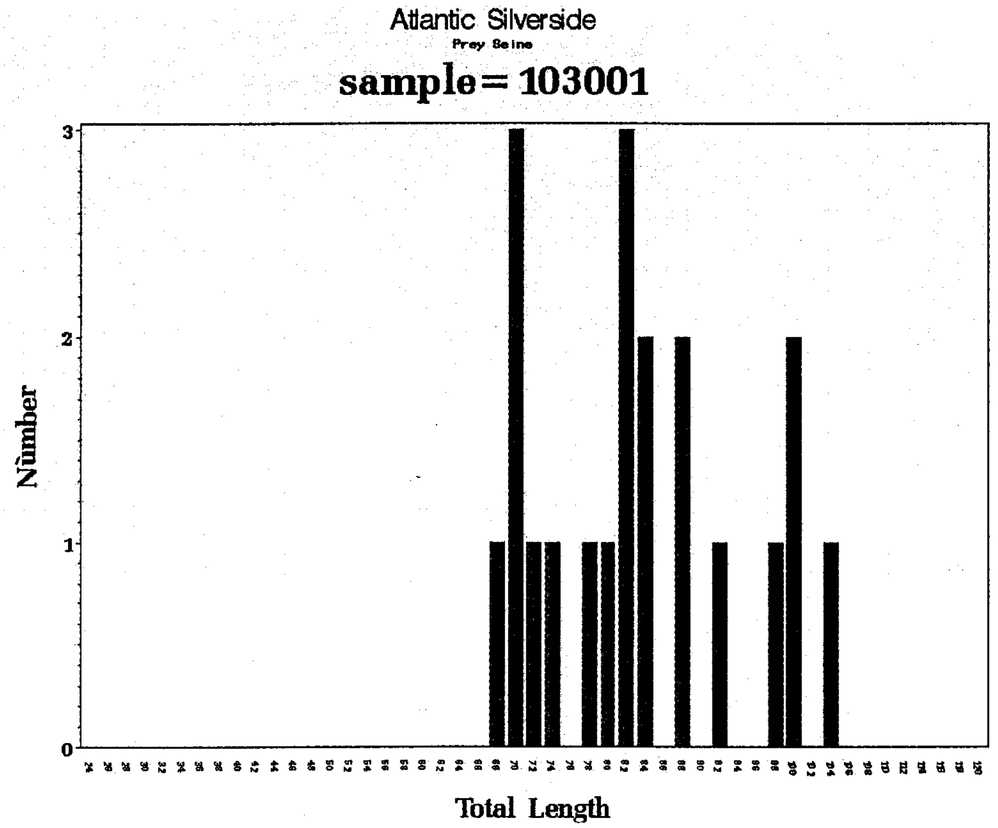




Striped Killifish

Prey Seine

sample= 100901

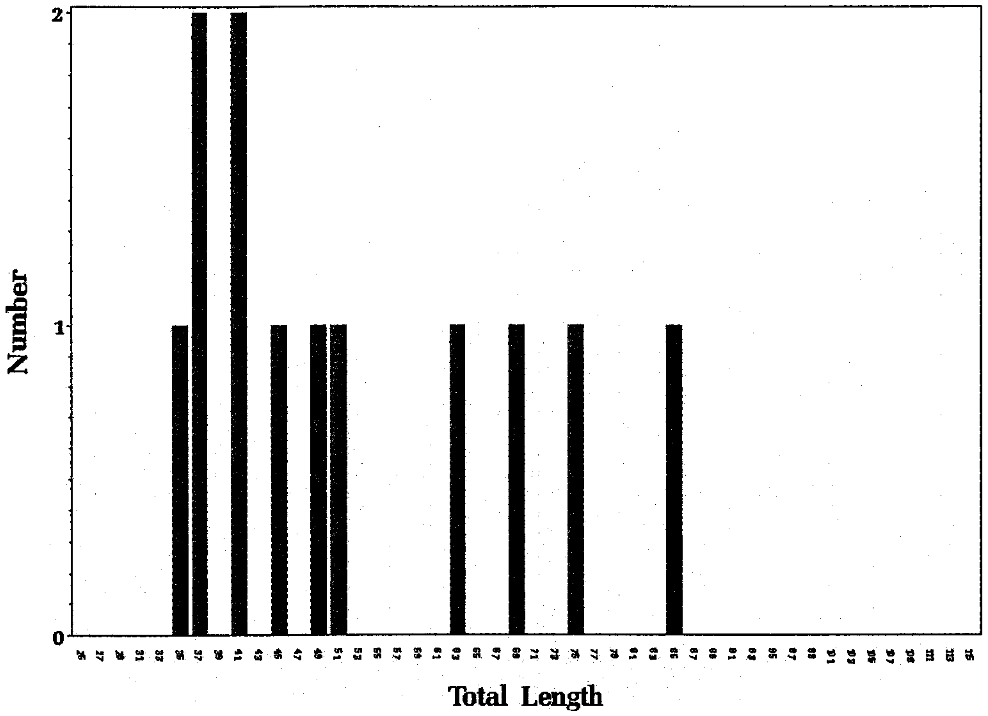


Atlantic Silverside

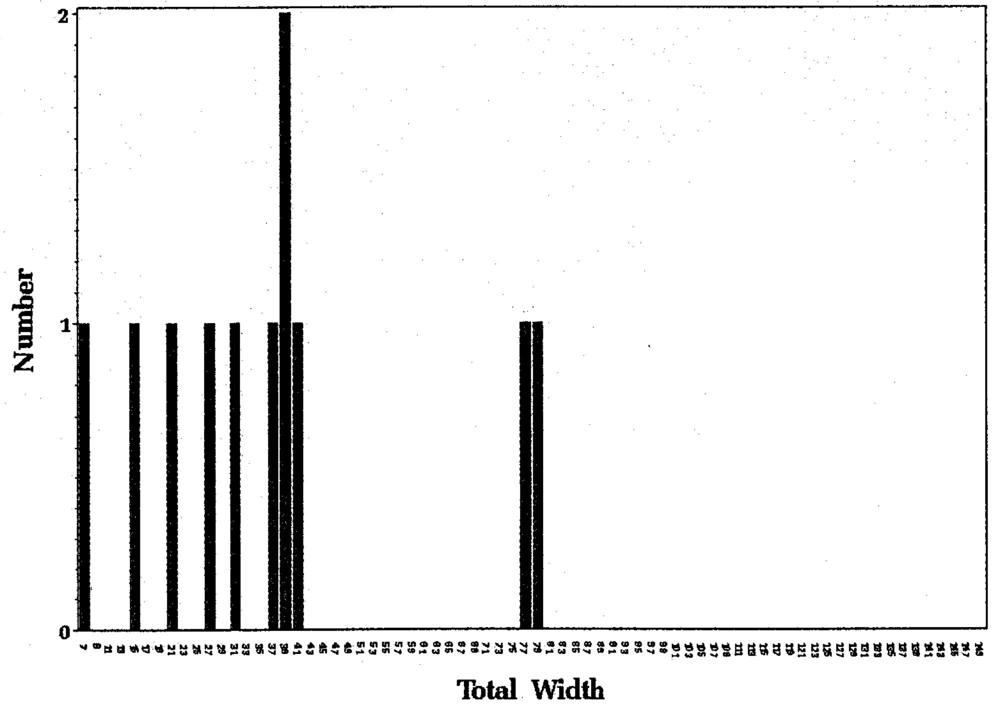
Prey Seine

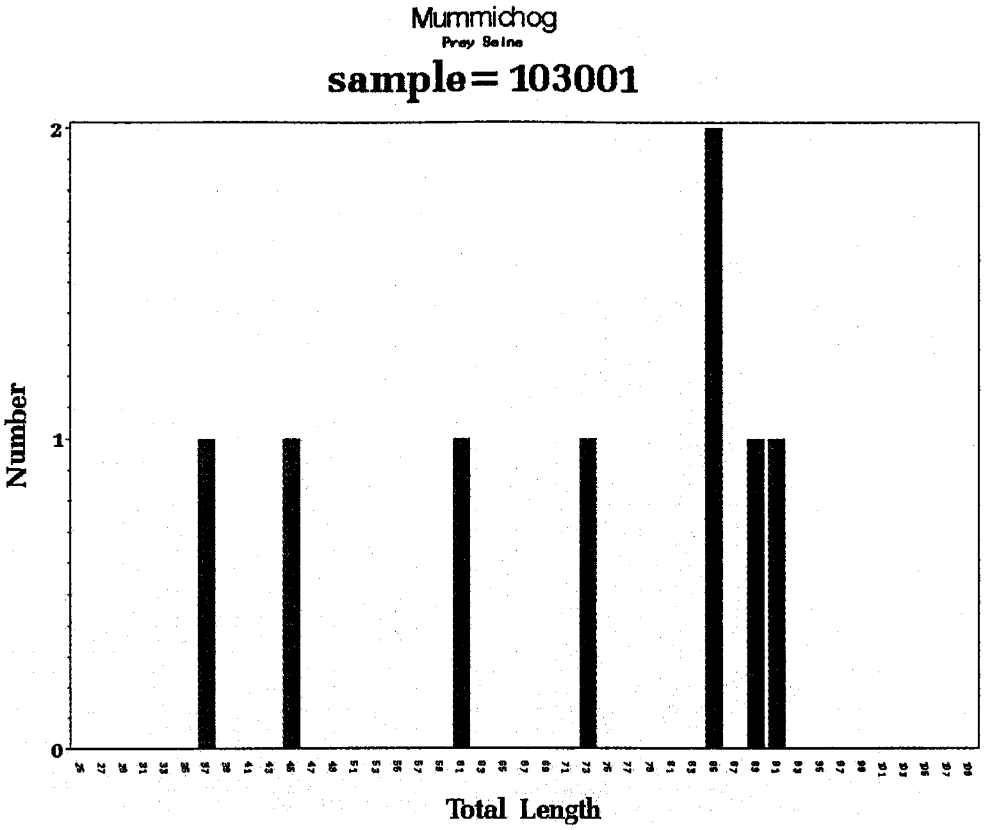
sample= 103001

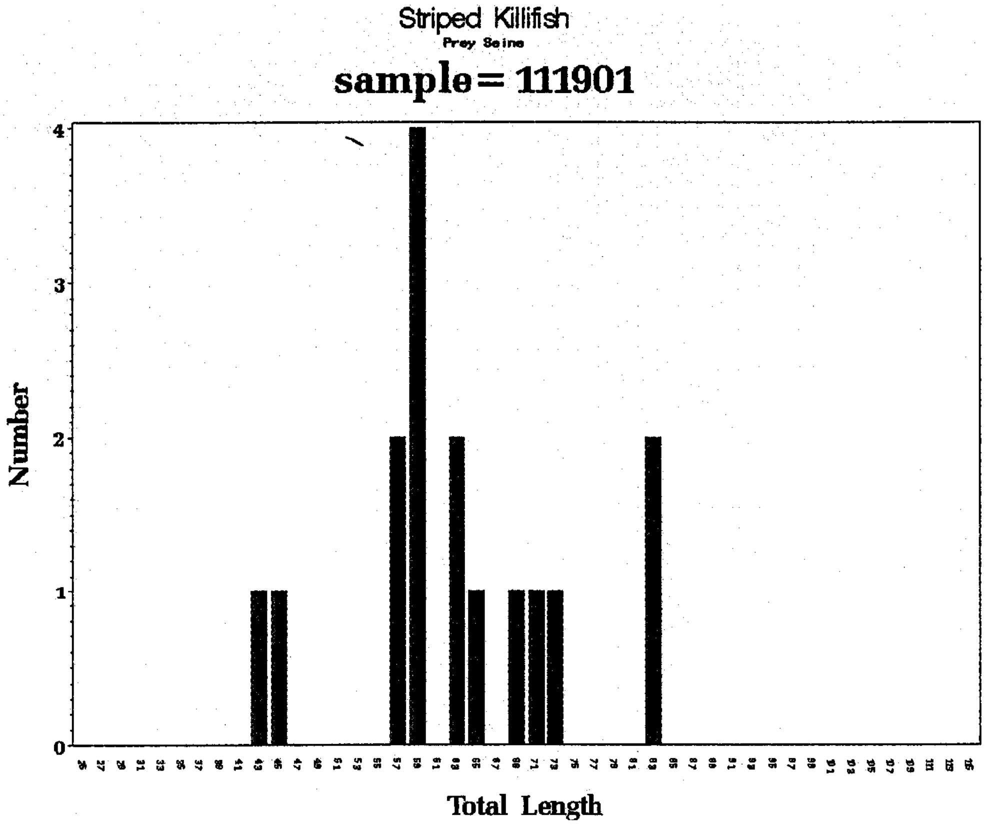
Striped Killifish
Prey Seine
sample= 103001

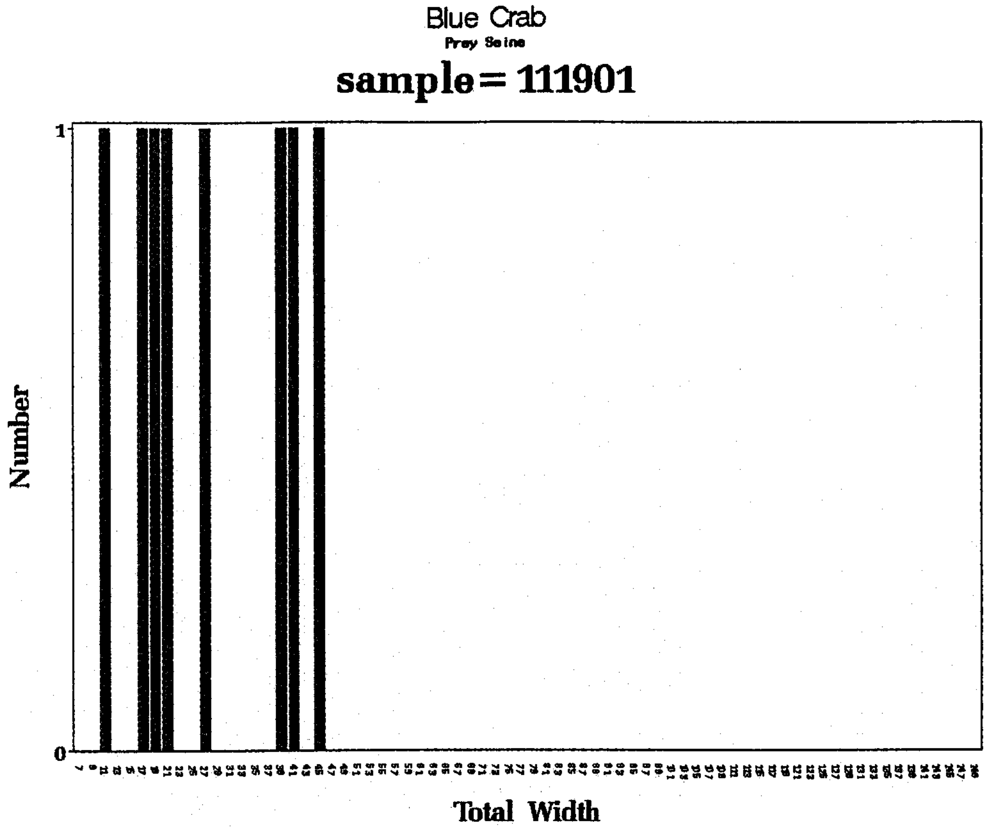


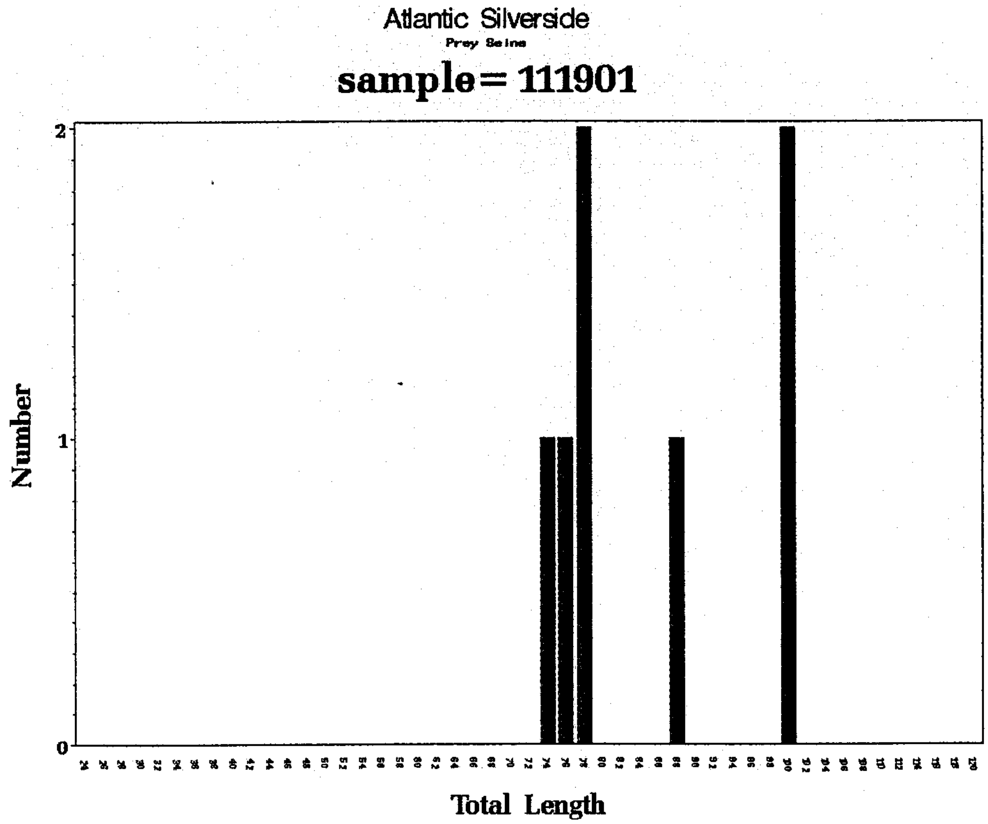
Blue Crab
Prey Seine
sample= 103001

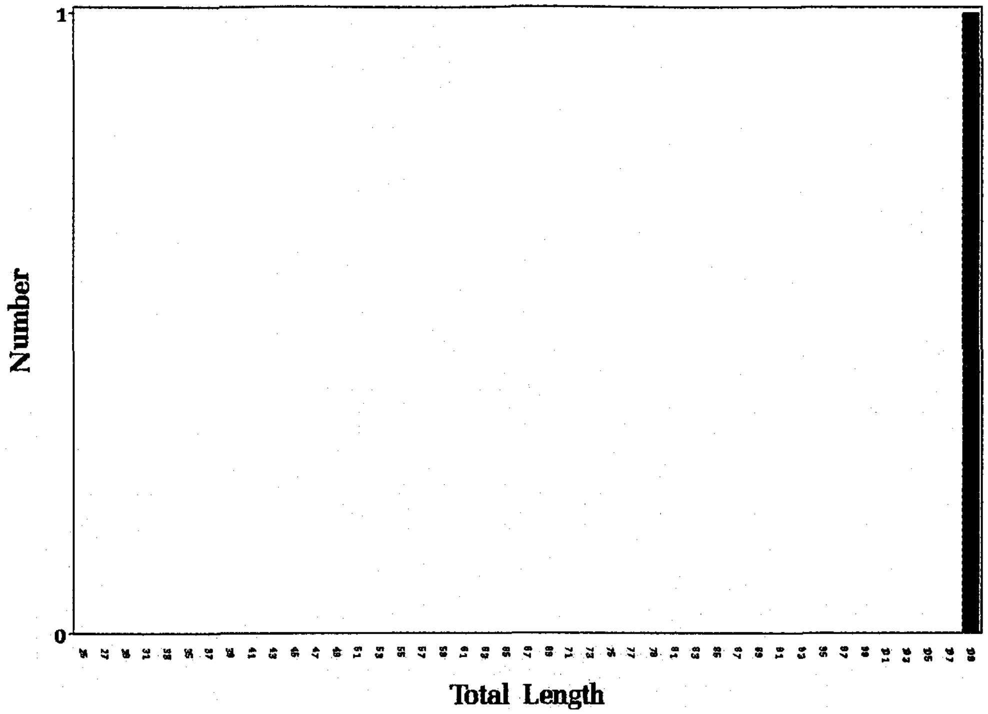



Mummichog
Prey Seine
sample= 103001
Number
0
1
2
Total Length


Striped Killifish
Prey Seine
sample= 111901
Number
0
1
2
3
4
Total Length


Blue Crab
Prey Seine
sample= 111901
Number
1
0
Total Width


Atlantic Silverside
Prey Seine
sample= 111901
Number
2
1
0
Total Length

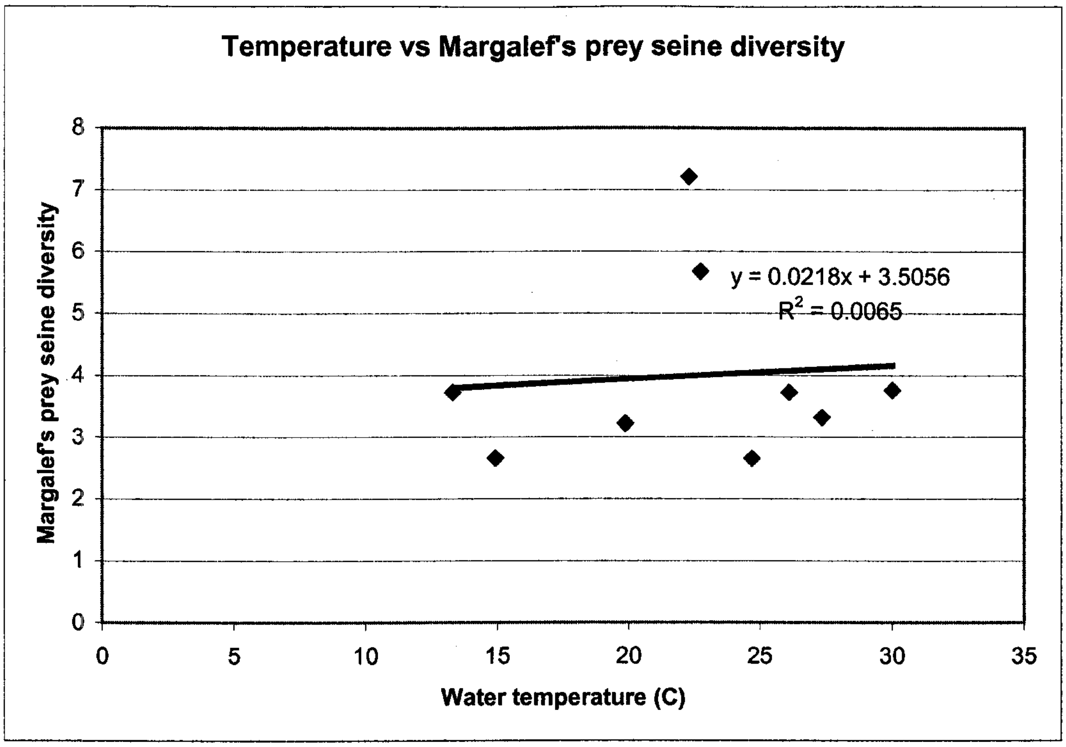


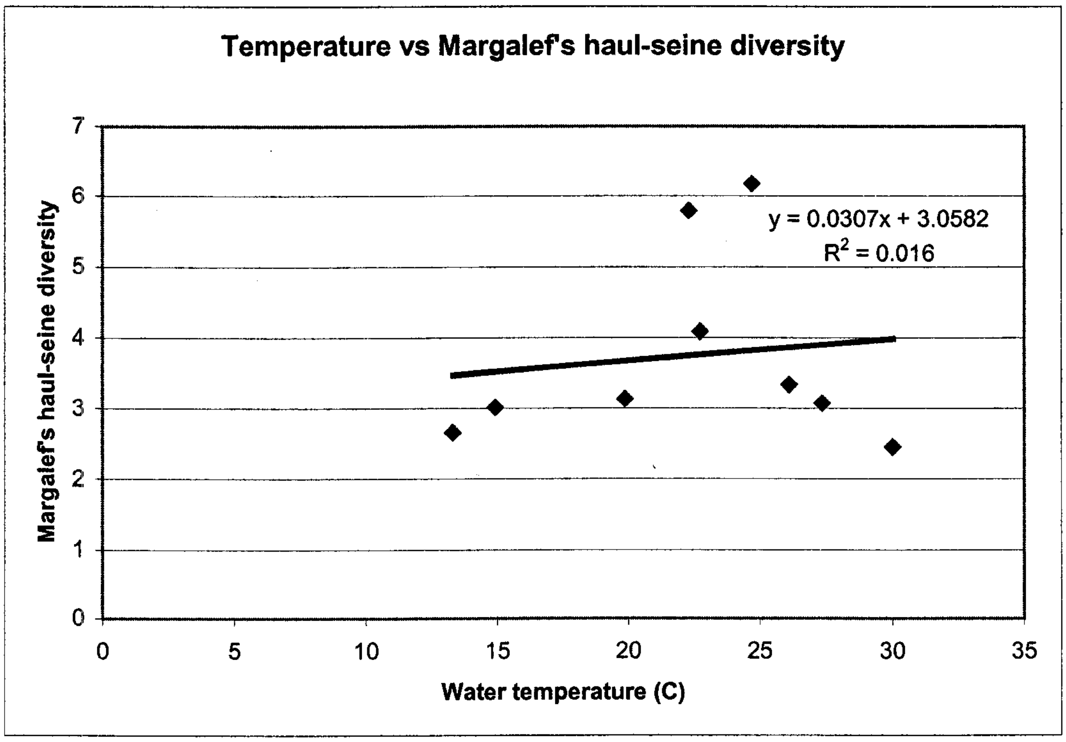
Mummichog

Prey Seine

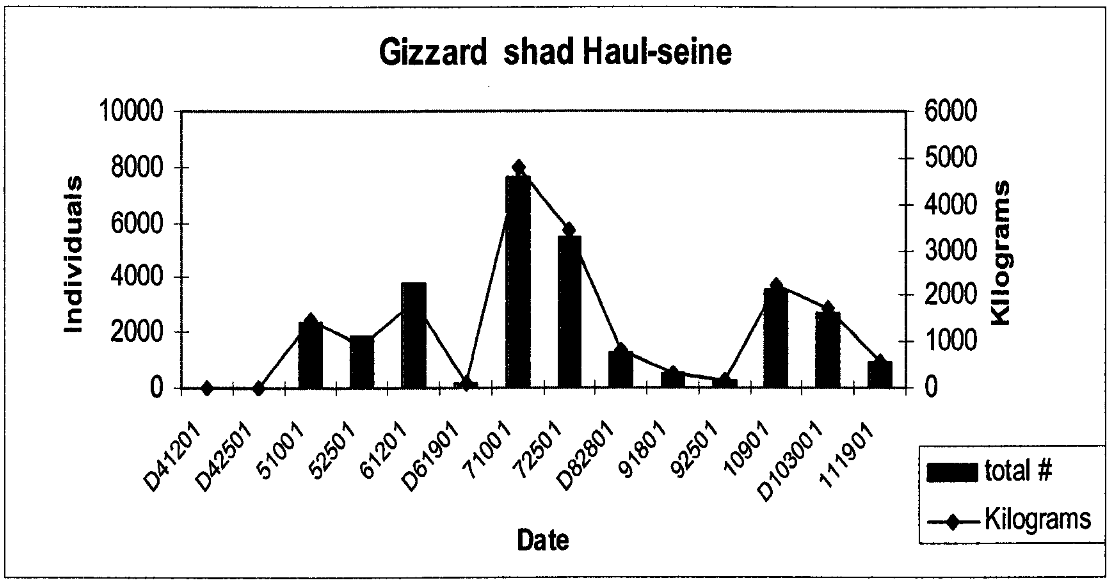
sample= 111901

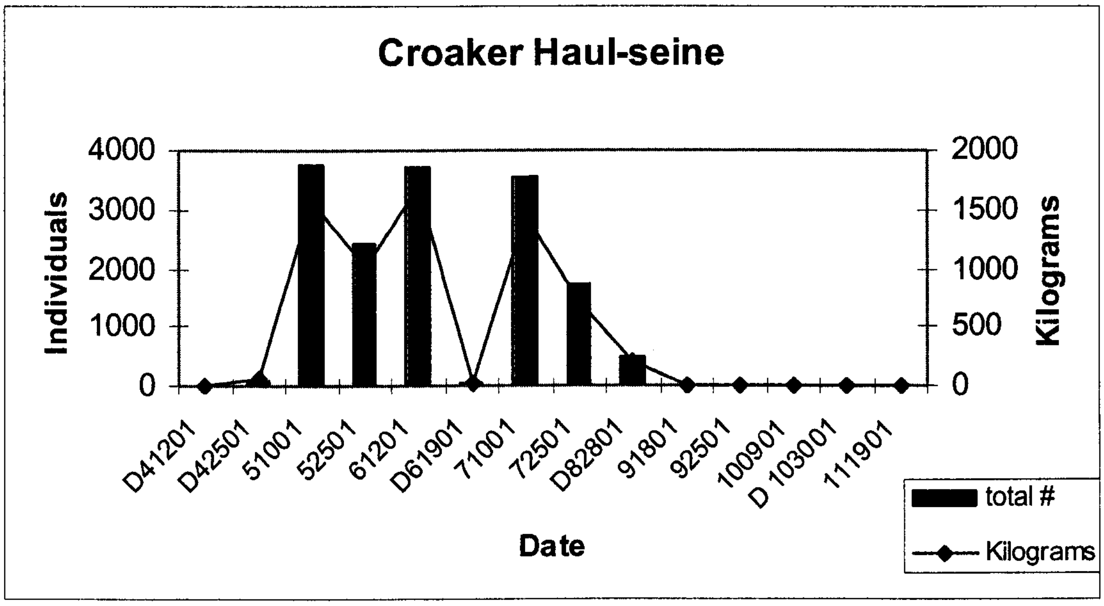
Appendix 4. This appendix contains graphic results and regression analysis of temperature vs. Margalef's diversity for prey and haul-seine samples.

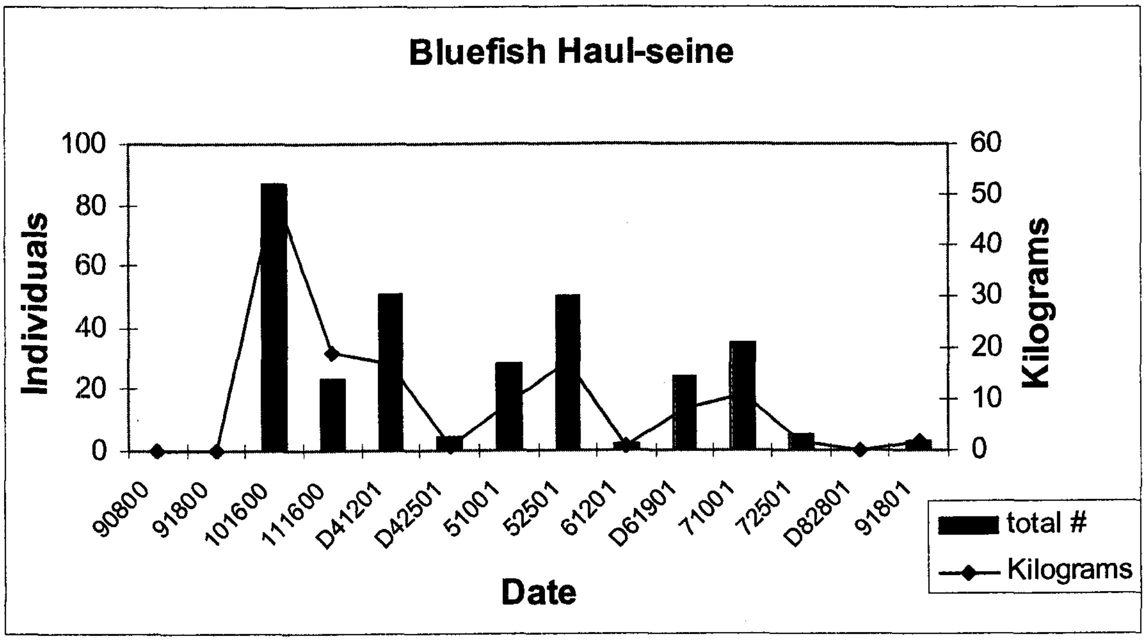

Temperature vs Margalef's prey seine diversity
Margalef's prey seine diversity
0
1
2
3
4
5
6
7
8
Water temperature (C)
0
5
10
15
20
25
30
35
y = 0.0218x + 3.5056
R^2 = 0.0065

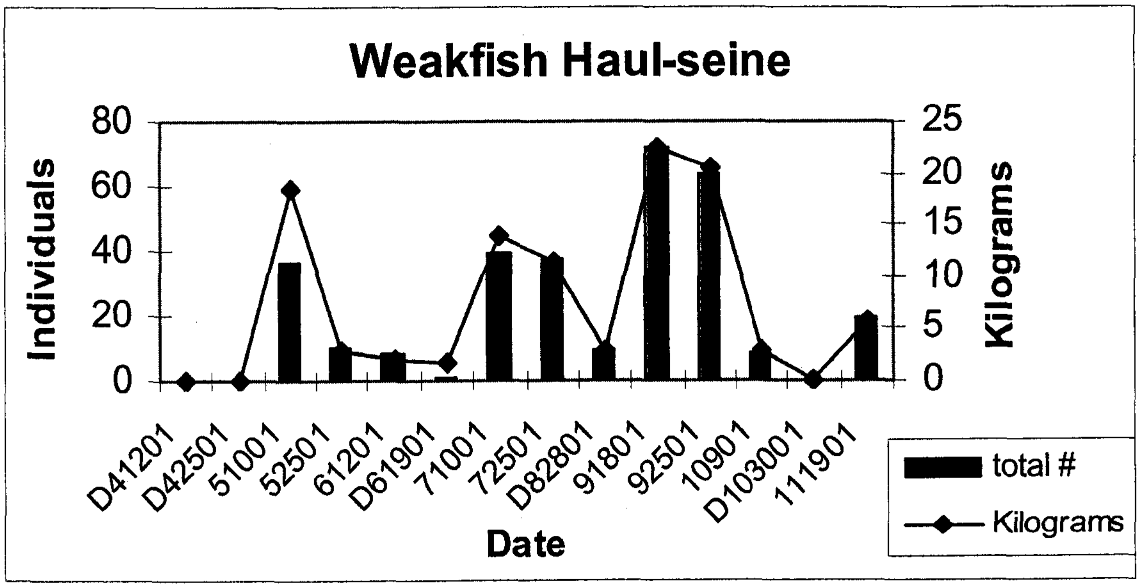

Temperature vs Margalef's haul-seine diversity
Margalef's haul-seine diversity
0
1
2
3
4
5
6
7
Water temperature (C)
0
5
10
15
20
25
30
35
y = 0.0307x + 3.0582
R^2 = 0.016

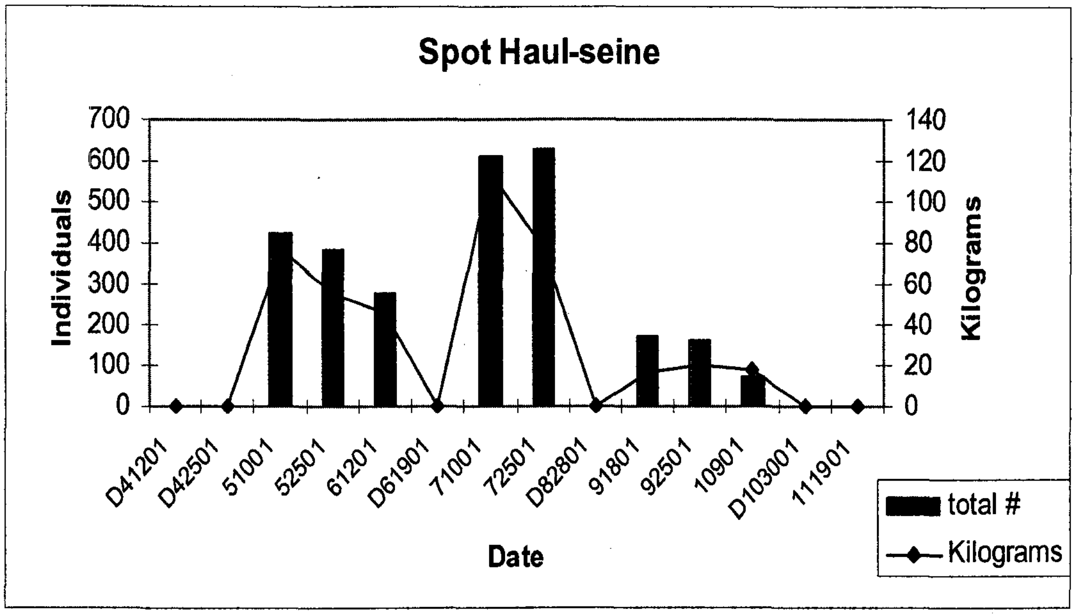
Appendix 5: Appendix 5 contains charts of abundance and mass for the eight most abundant species captured in the haul-seine. Abundance estimates do not include gear efficiency estimates. Daylight samples are marked with a D.

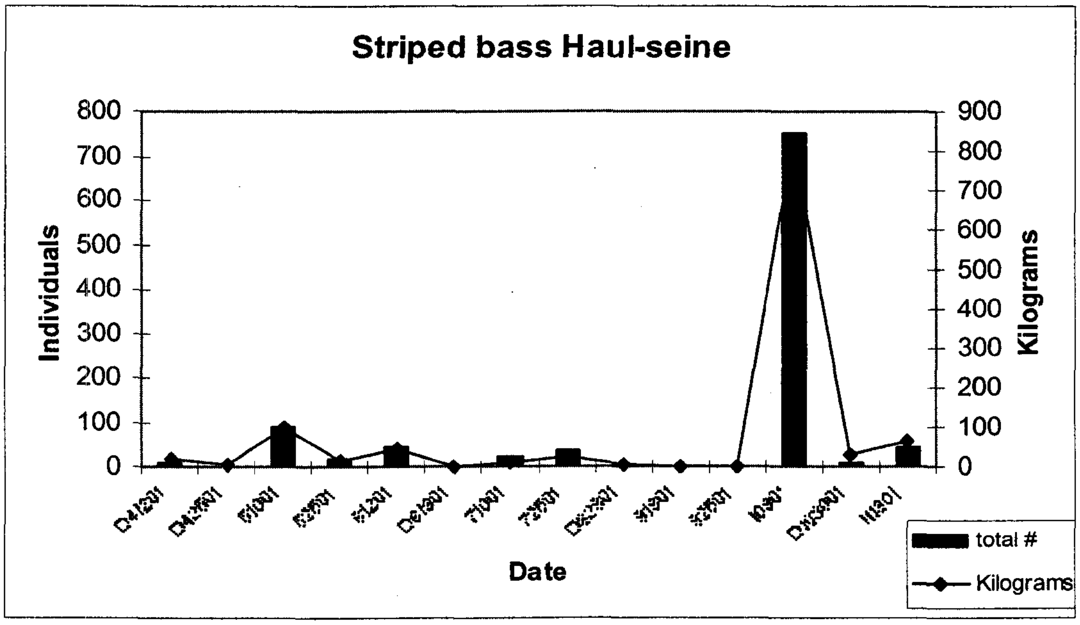


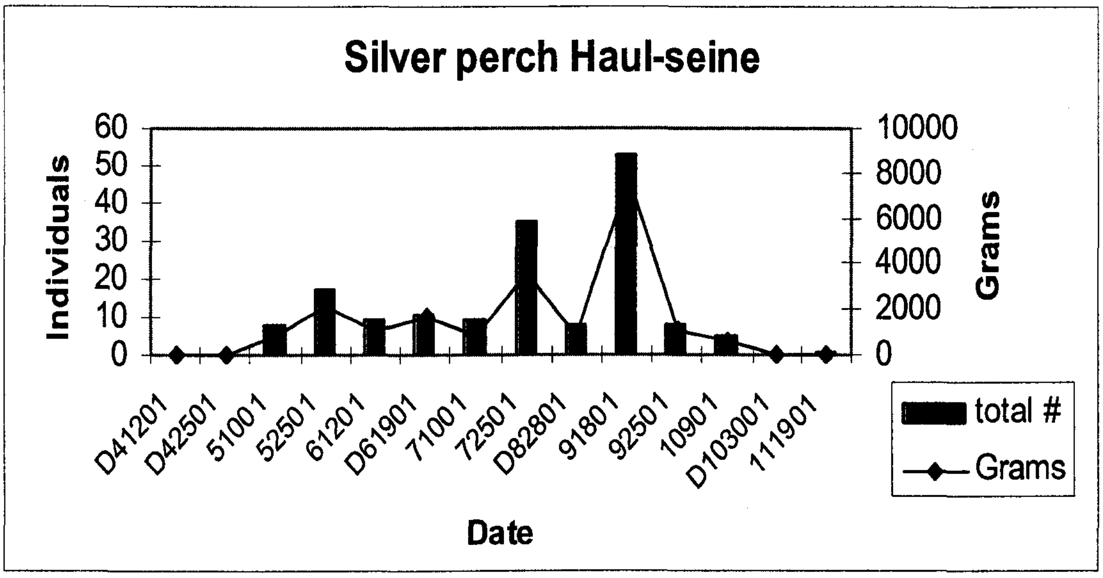


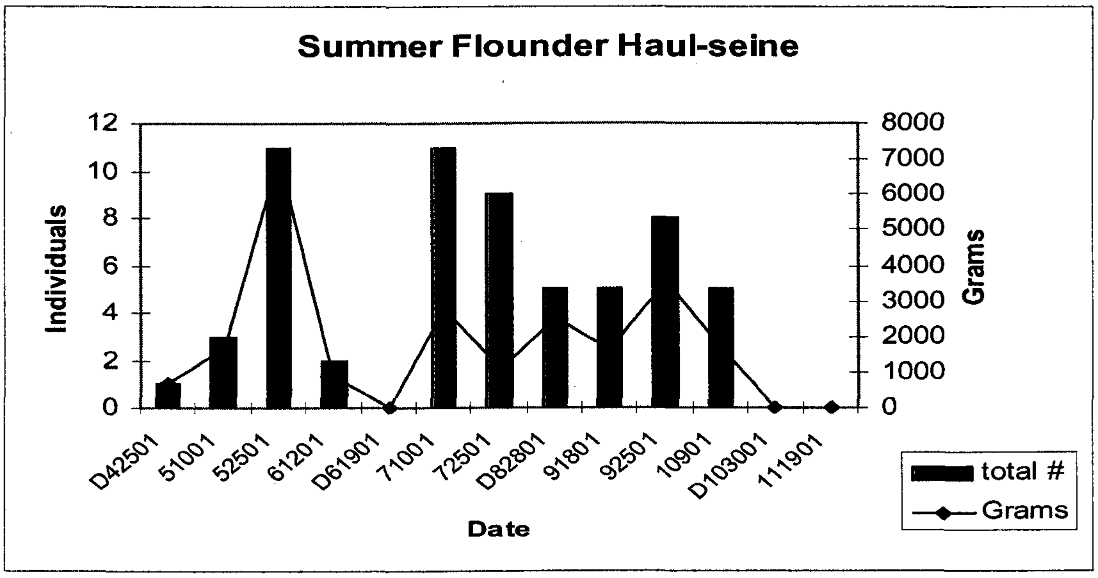

Bluefish Haul-seine
Individuals
100
80
60
40
20
0
Kilograms
60
50
40
30
20
10
0
90800
91800
101600
111600
D41201
D42501
51001
52501
61201
D61901
71001
72501
D82801
91801
Date
total #
Kilograms


Weakfish Haul-seine
Individuals
80
60
40
20
0
Kilograms
25
20
15
10
5
0
D41201
D42501
51001
52501
61201
D61901
71001
72501
D82801
91801
92501
10901
D103001
111901
Date
total #
Kilograms


Spot Haul-seine
Individuals
0
100
200
300
400
500
600
700
Kilograms
0
20
40
60
80
100
120
140
D41201
D42501
51001
52501
61201
D61901
71001
72501
D82801
91801
92501
10901
D103001
111901
Date
total #
Kilograms


Striped bass Haul-seine
Individuals
0
100
200
300
400
500
600
700
800
Kilograms
0
100
200
300
400
500
600
700
800
900
D41201
D61901
71001
Date
total #
Kilograms

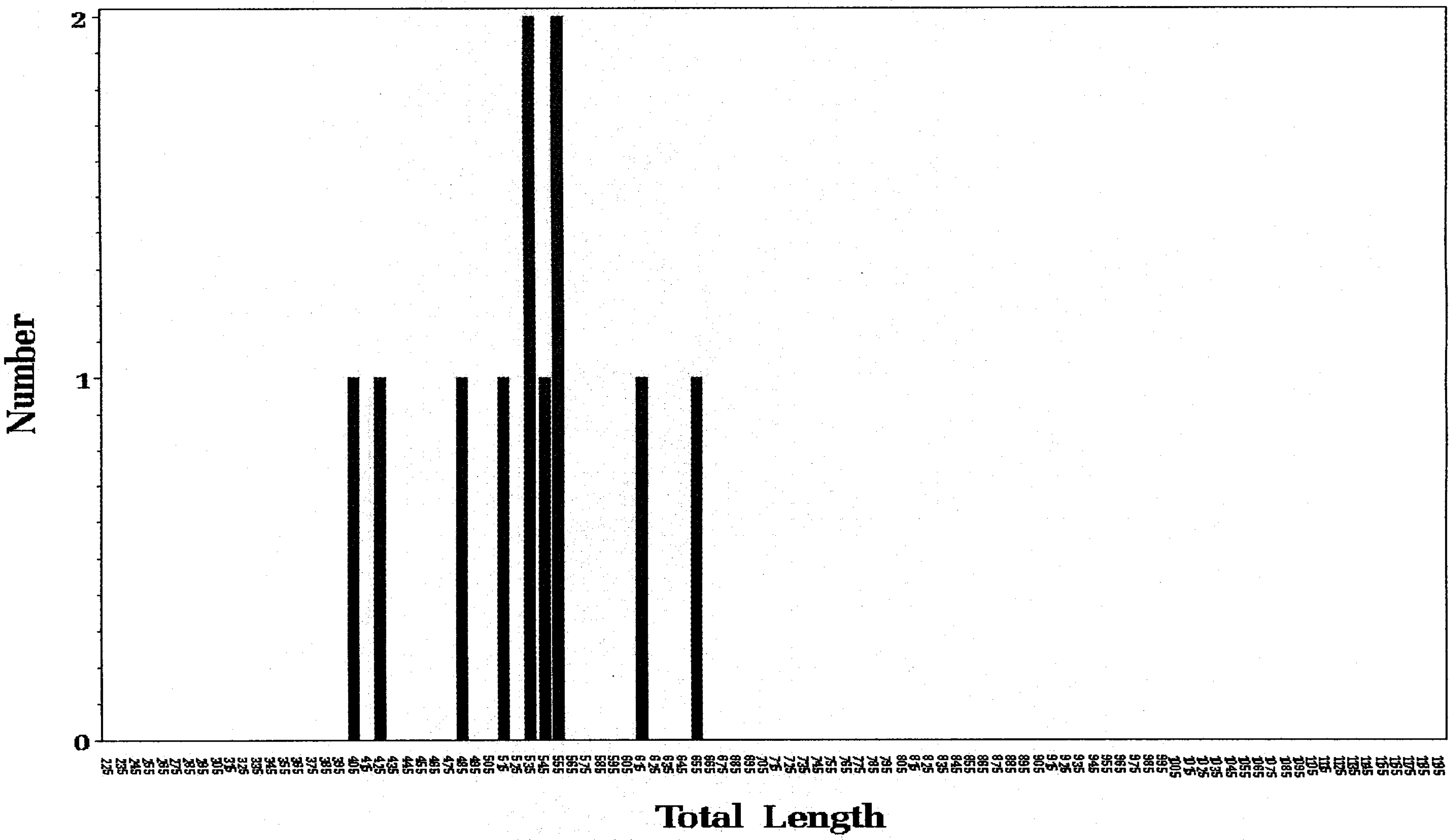

Silver perch Haul-seine
Individuals
60
50
40
30
20
10
0
Grams
10000
8000
6000
4000
2000
0
D41201
D42501
51001
52501
61201
D61901
71001
72501
D82801
91801
92501
10901
D103001
111901
Date
total #
Grams

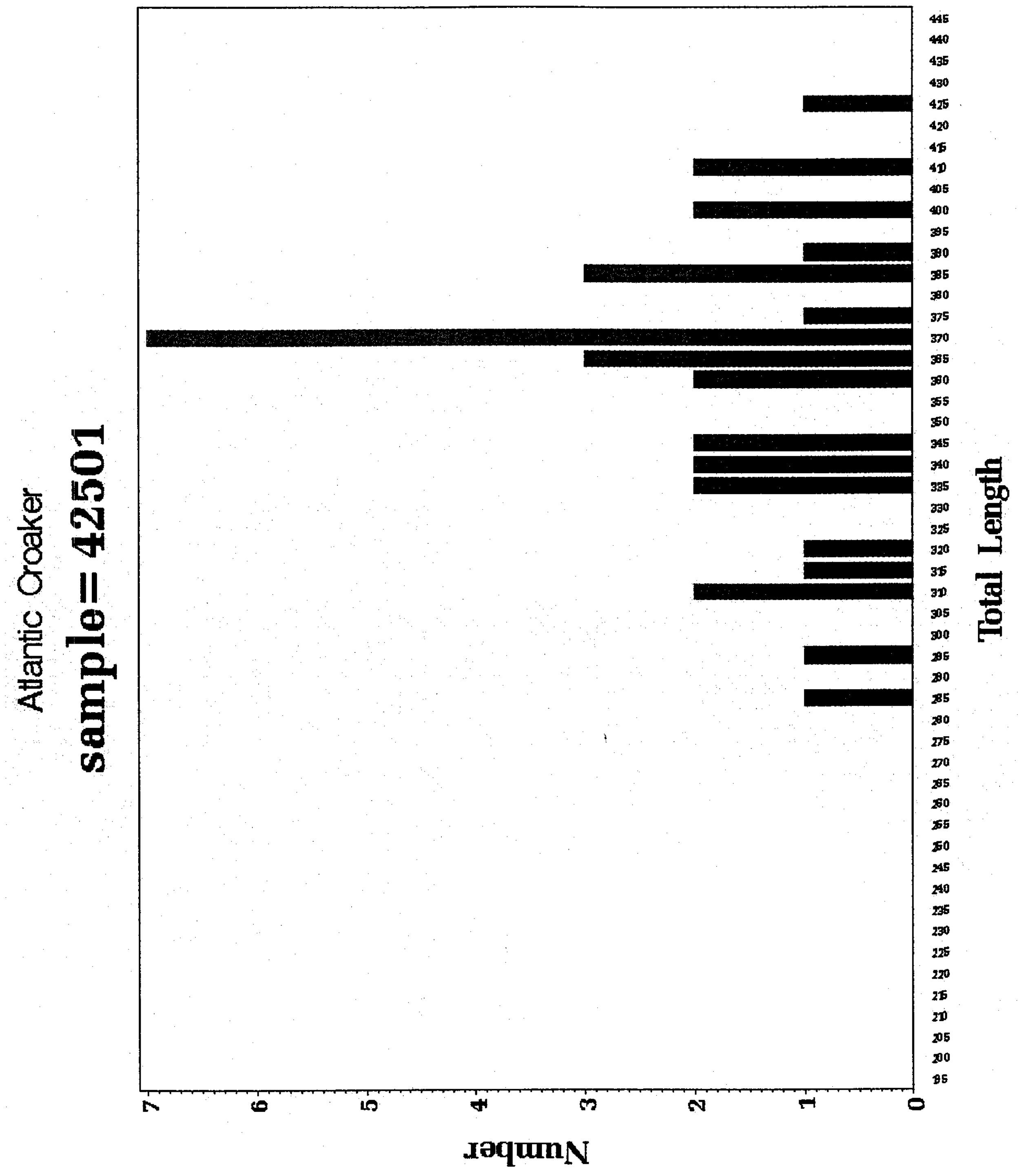

Summer Flounder Haul-seine
Individuals
12
10
8
6
4
2
0
Grams
8000
7000
6000
5000
4000
3000
2000
1000
0
D42501
51001
52501
61201
D61901
71001
72501
D82801
91801
92501
10901
D103001
111901
Date
total #
Grams

Appendix 6. This appendix contains the size distributions of the six most abundant species captured in the haul-seine. They are presented in order of sample date and then relative abundance on that date. If not listed species did not occur on date.

Striped Bass

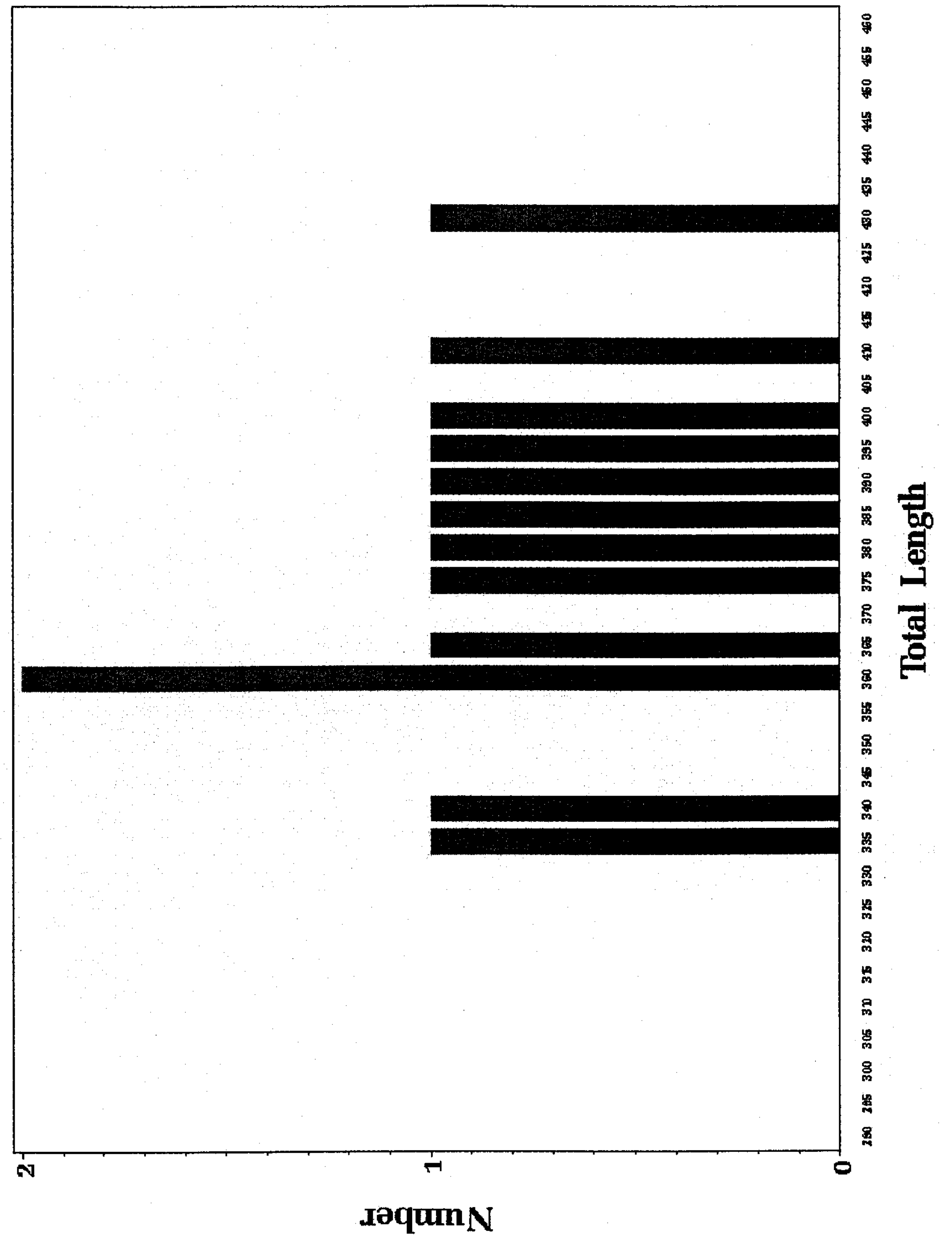
sample= 41201

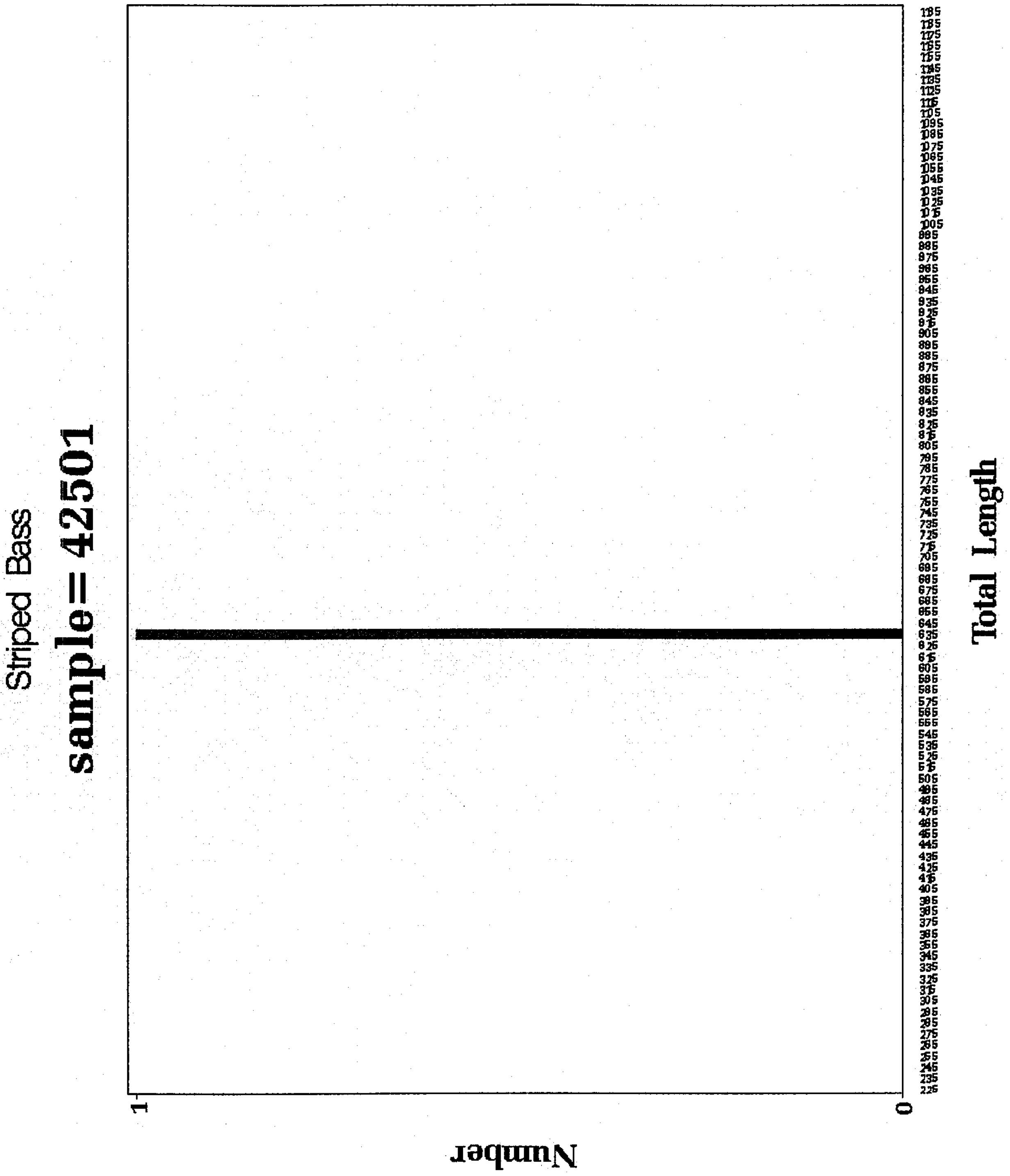


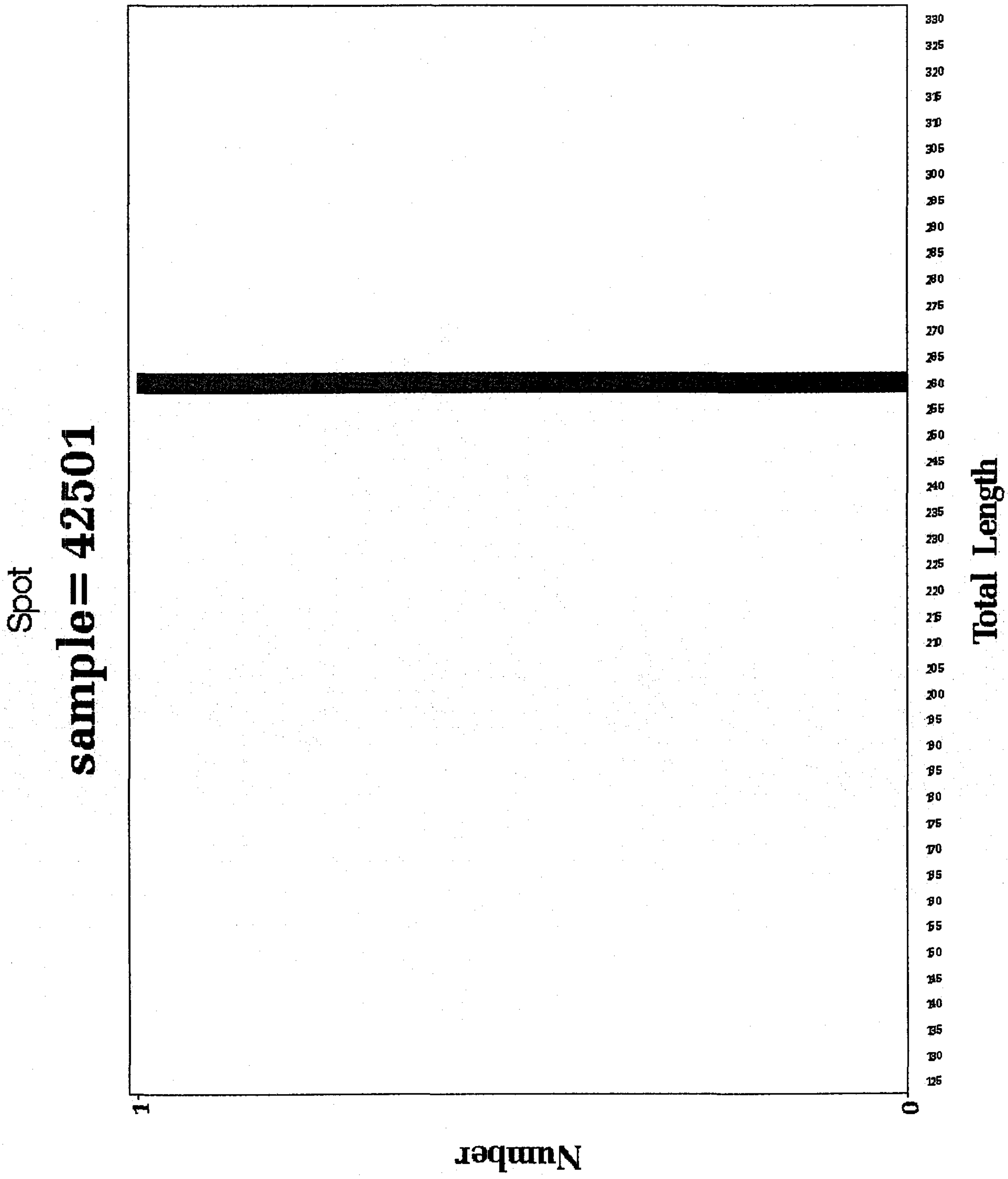

Atlantic Croaker
sample= 42501
Number
0
1
2
3
4
5
6
7
Total Length
195
200
205
210
215
220
225
230
235
240
245
250
255
260
265
270
275
280
285
290
295
300
305
310
315
320
325
330
335
340
345
350
355
360
365
370
375
380
385
390
395
400
405
410
415
420
425
430
435
440
445

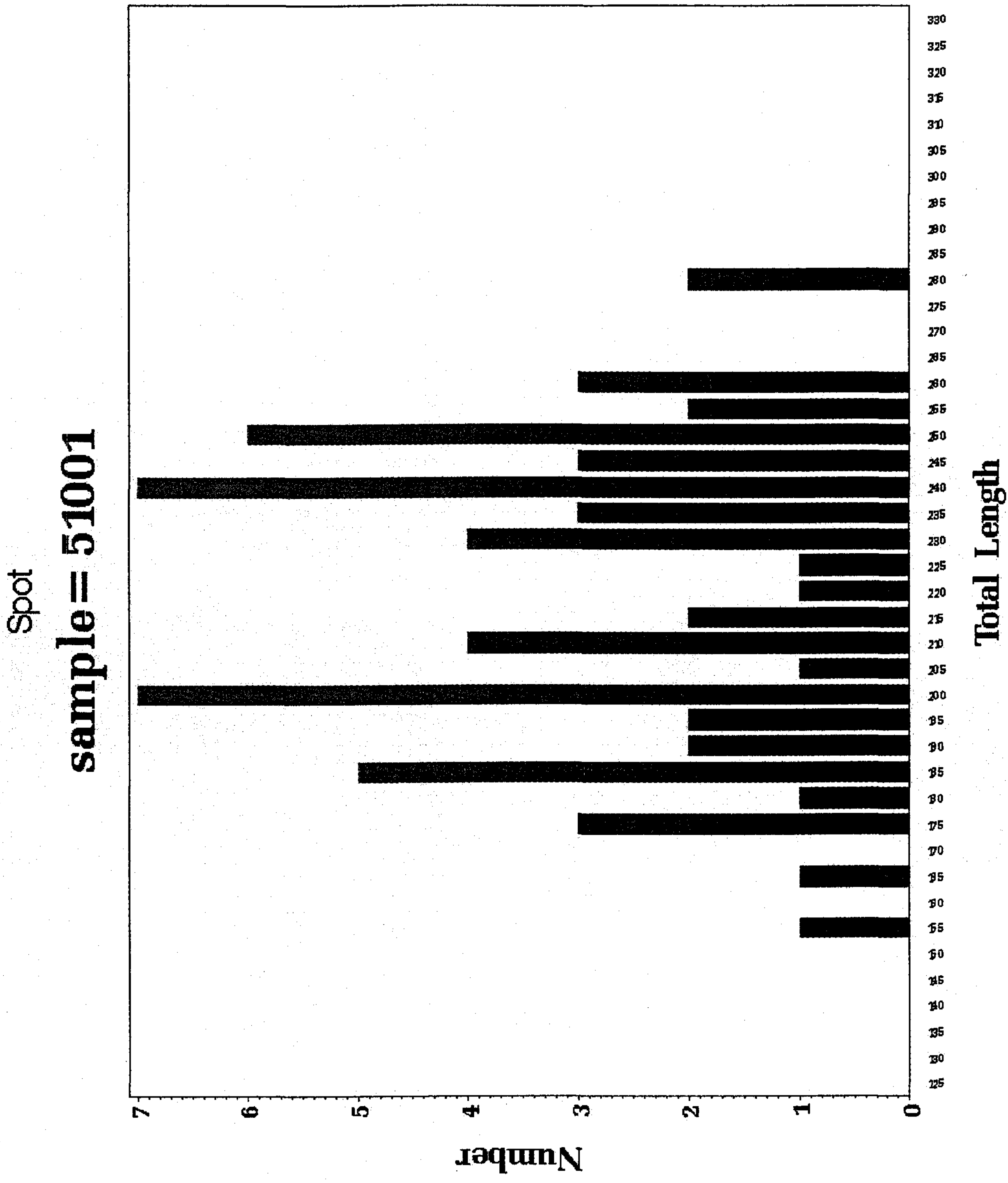
Gizzard Shad

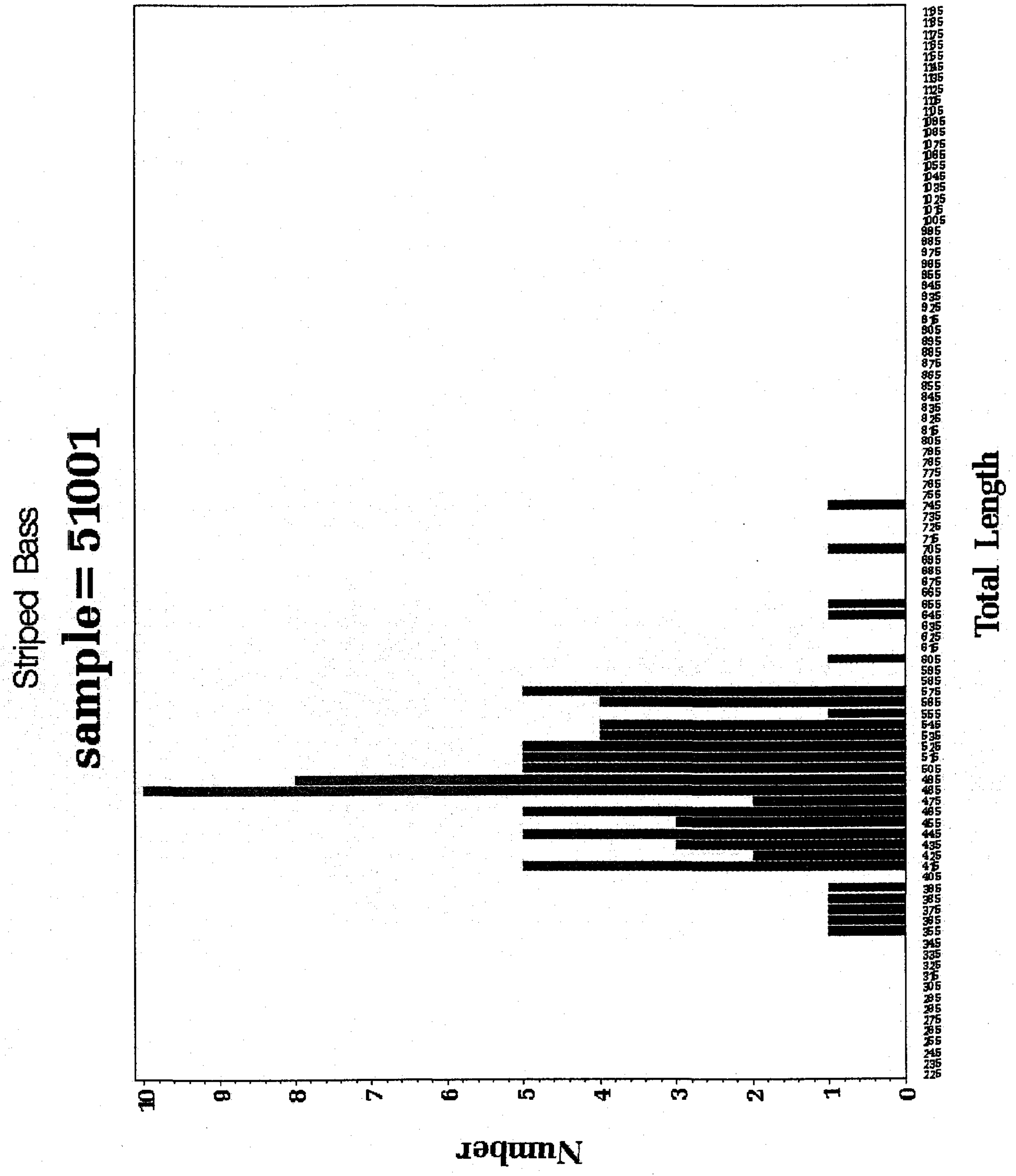
sample= 42501




Striped Bass
sample= 42501
Number
1
0
Total Length
225
1195

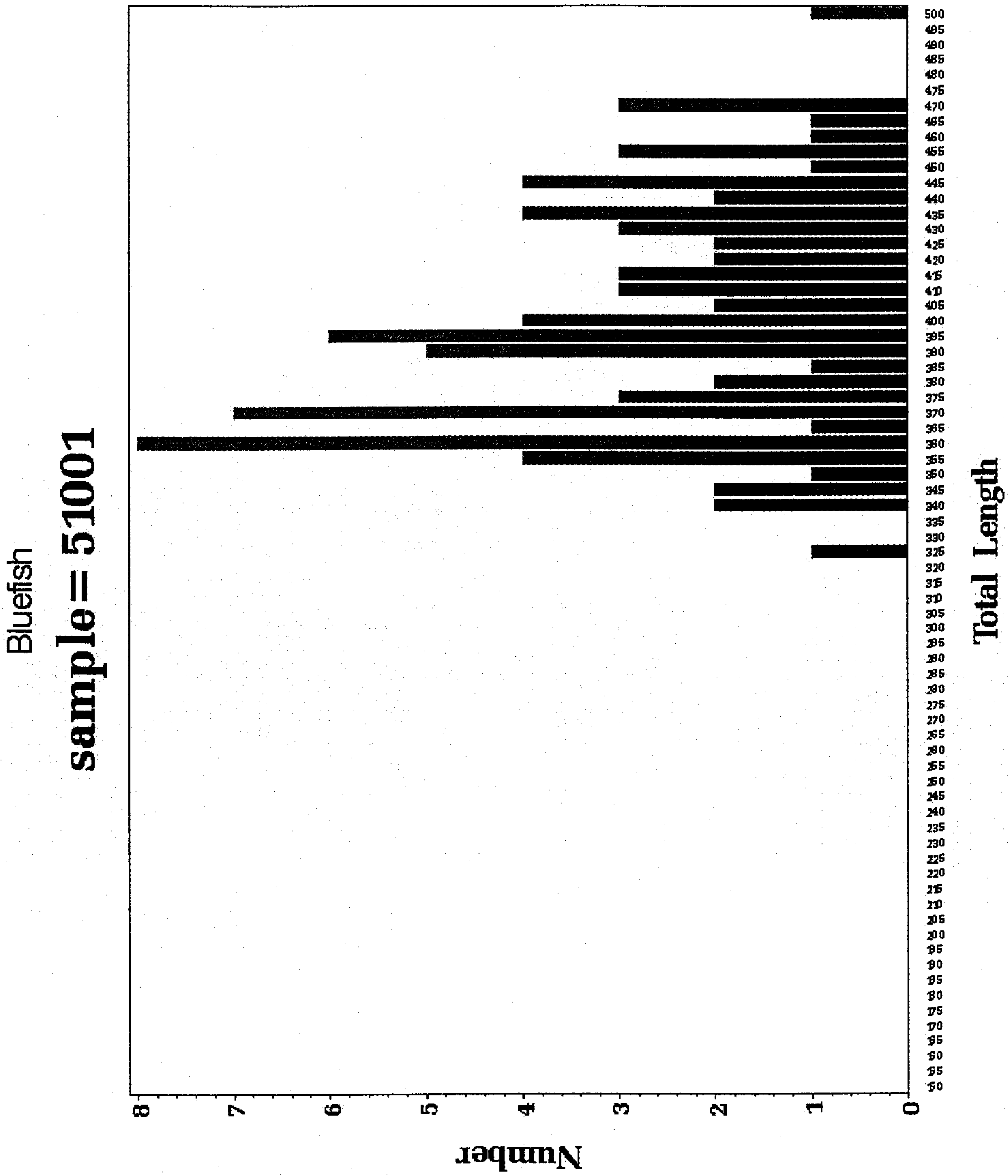

Spot
sample= 42501
Total Length
Number
0
1
125
130
135
140
145
150
155
160
165
170
175
180
185
190
195
200
205
210
215
220
225
230
235
240
245
250
255
260
265
270
275
280
285
290
295
300
305
310
315
320
325
330

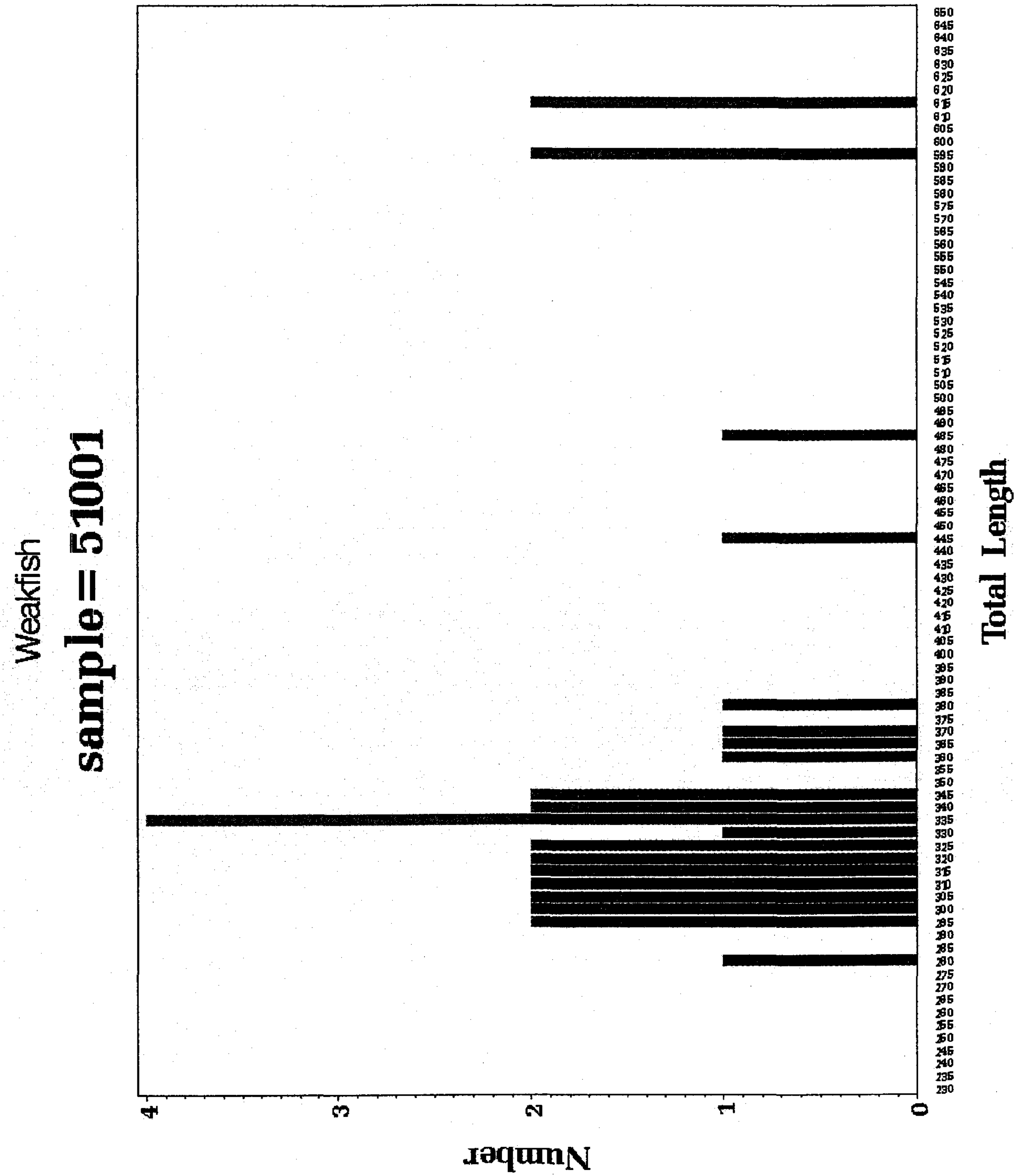

Spot
sample= 51001
Number
0
1
2
3
4
5
6
7
Total Length
125
130
135
140
145
150
155
160
165
170
175
180
185
190
195
200
205
210
215
220
225
230
235
240
245
250
255
260
265
270
275
280
285
290
295
300
305
310
315
320
325
330

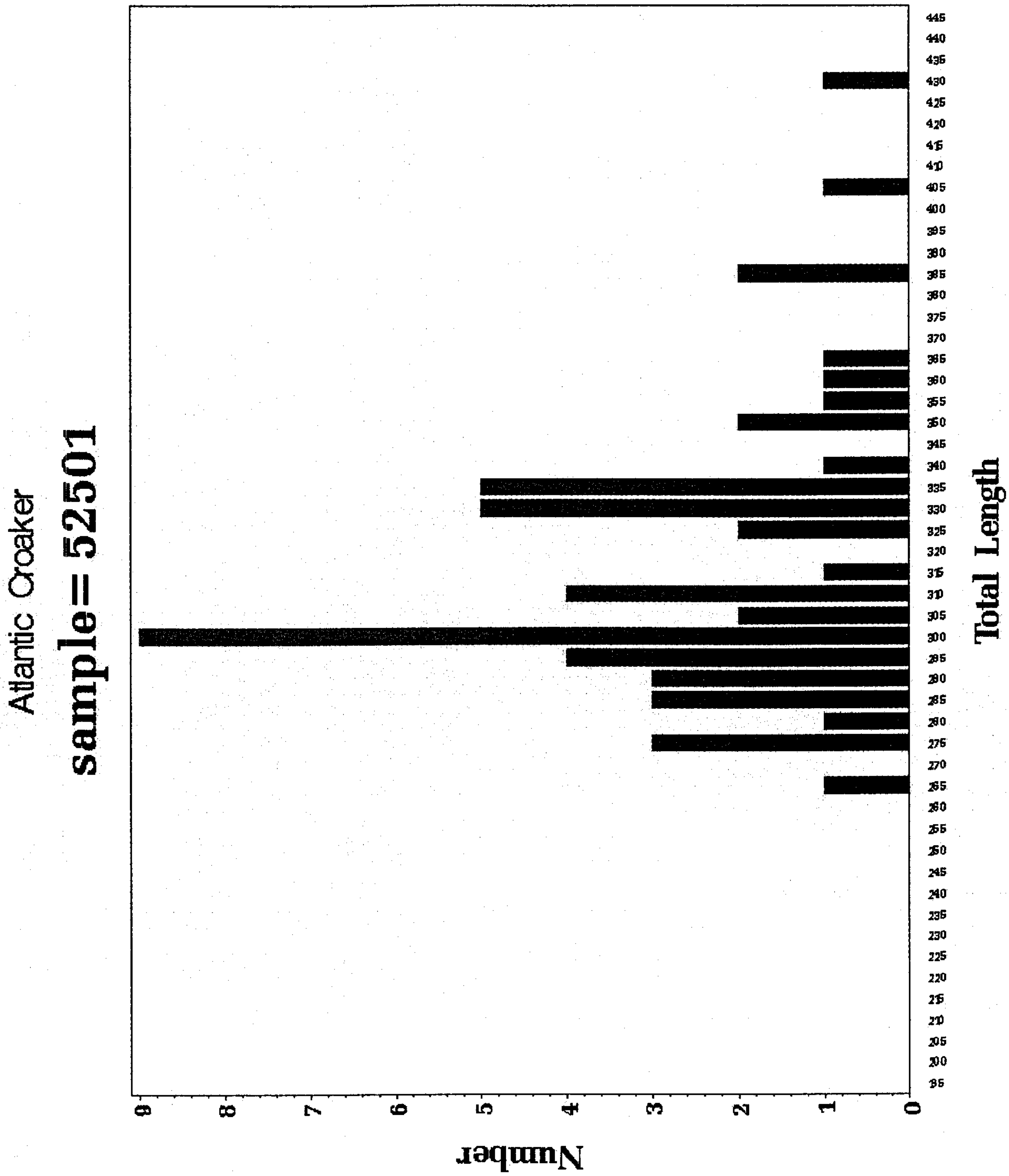


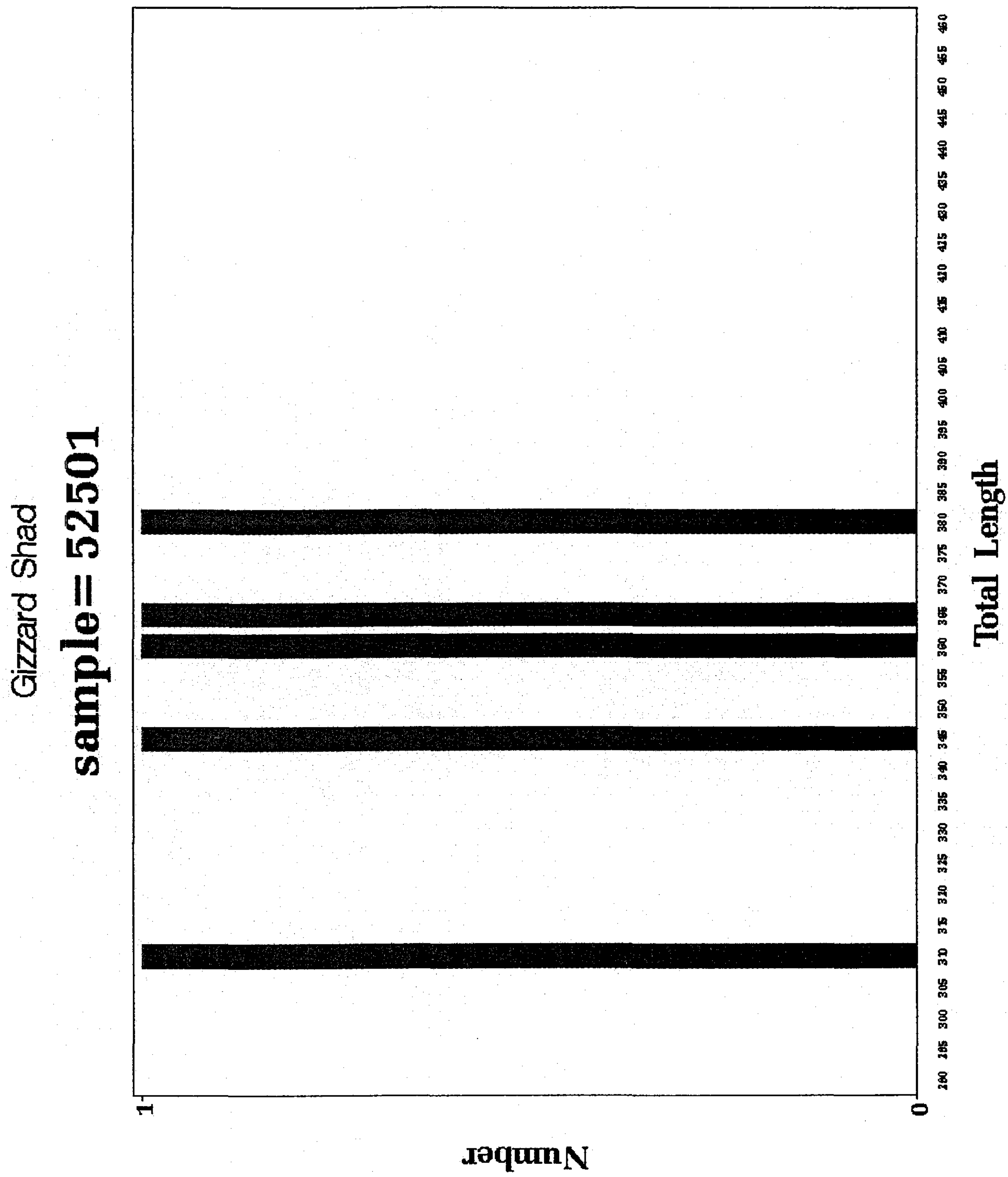
Striped Bass

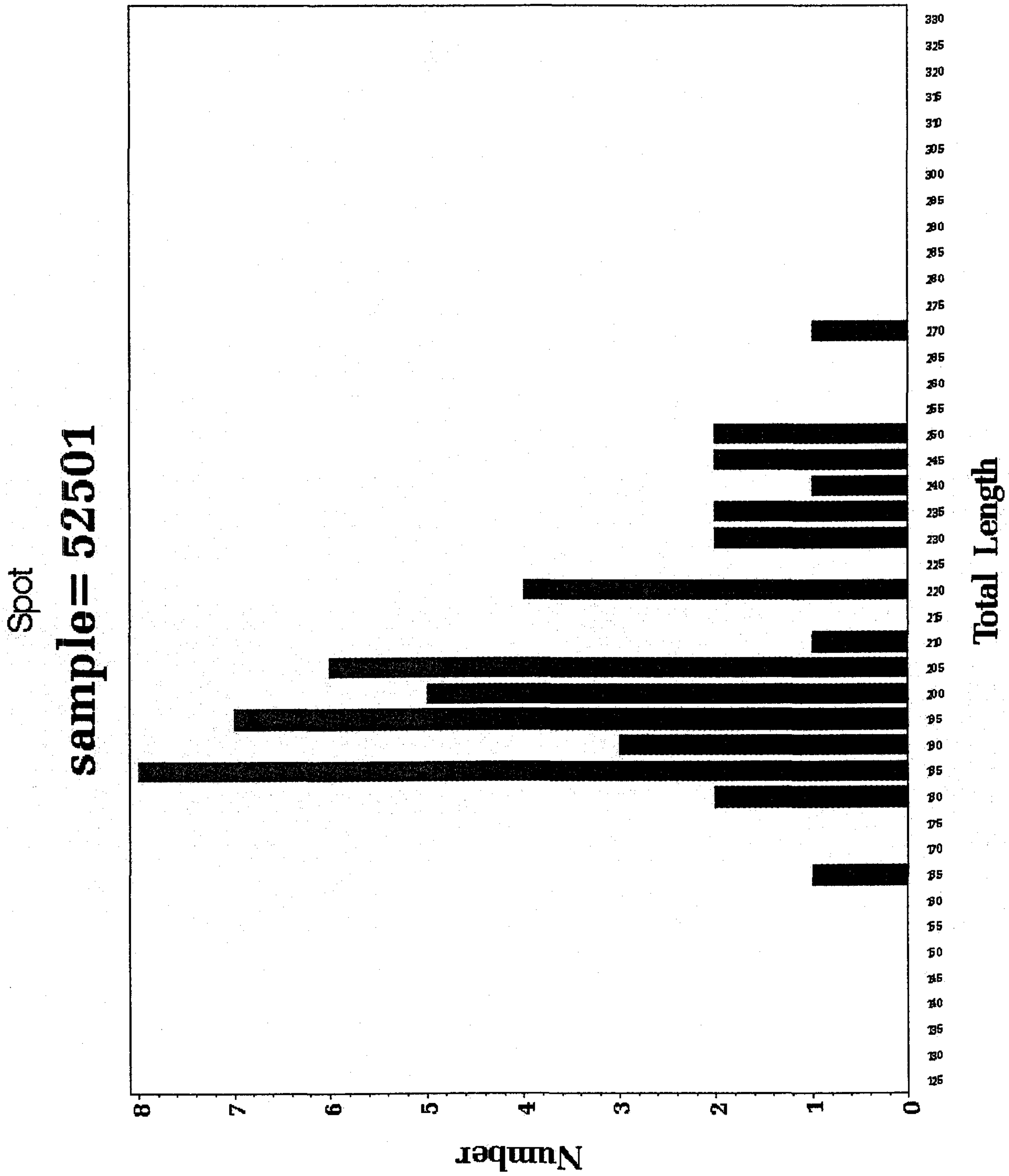
sample=51001


Bluefish
sample=51001
Total Length
Number
0
1
2
3
4
5
6
7
8
150
200
250
300
350
400
450
500


Weakfish
sample=51001
Number
0
1
2
3
4
Total Length
230
235
240
245
250
255
260
265
270
275
280
285
290
295
300
305
310
315
320
325
330
335
340
345
350
355
360
365
370
375
380
385
390
395
400
405
410
415
420
425
430
435
440
445
450
455
460
465
470
475
480
485
490
495
500
505
510
515
520
525
530
535
540
545
550
555
560
565
570
575
580
585
590
595
600
605
610
615
620
625
630
635
640
645
650

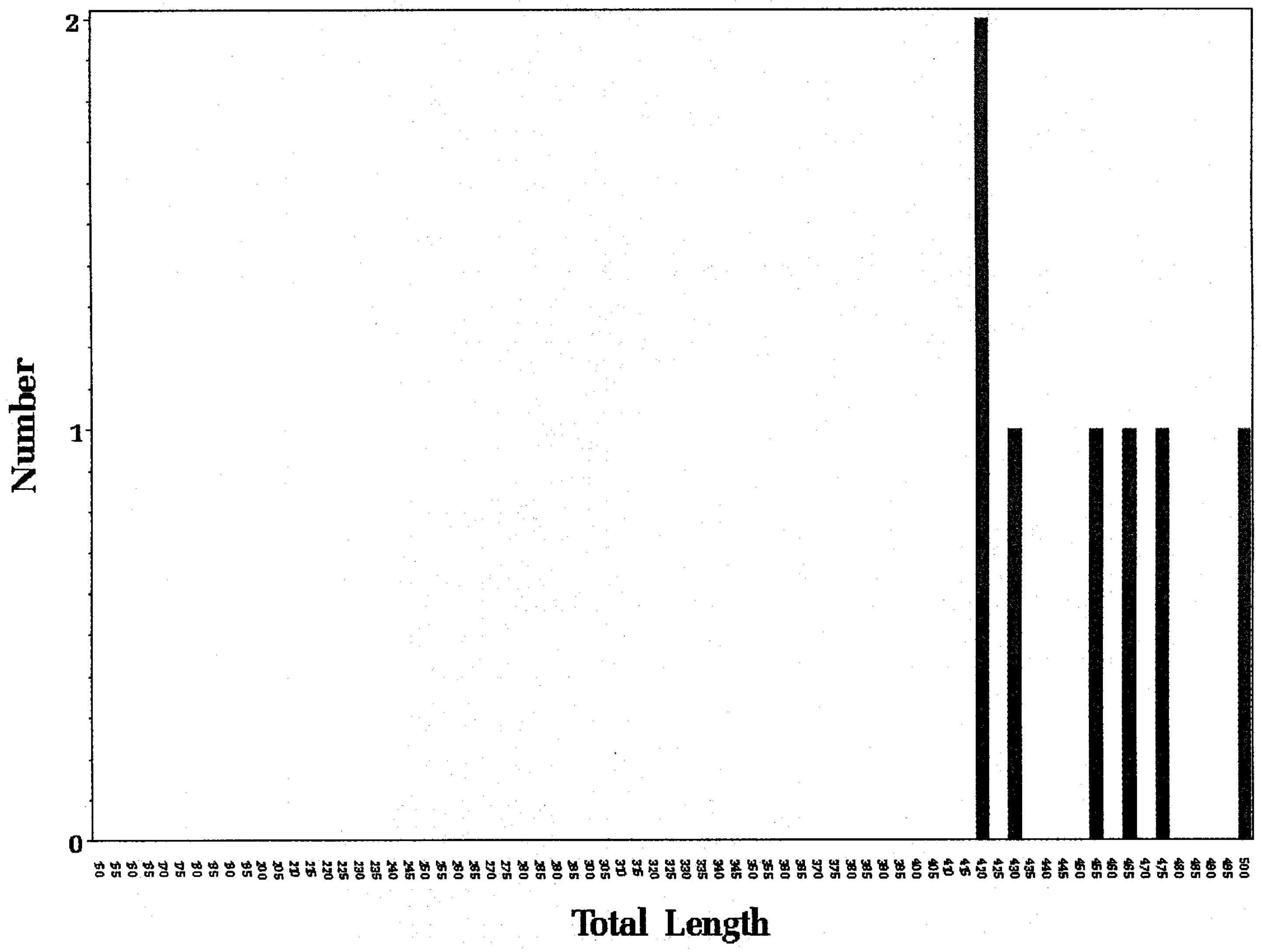

Atlantic Croaker
sample= 52501
Number
0
1
2
3
4
5
6
7
8
9
Total Length
195
200
205
210
215
220
225
230
235
240
245
250
255
260
265
270
275
280
285
290
295
300
305
310
315
320
325
330
335
340
345
350
355
360
365
370
375
380
385
390
395
400
405
410
415
420
425
430
435
440
445

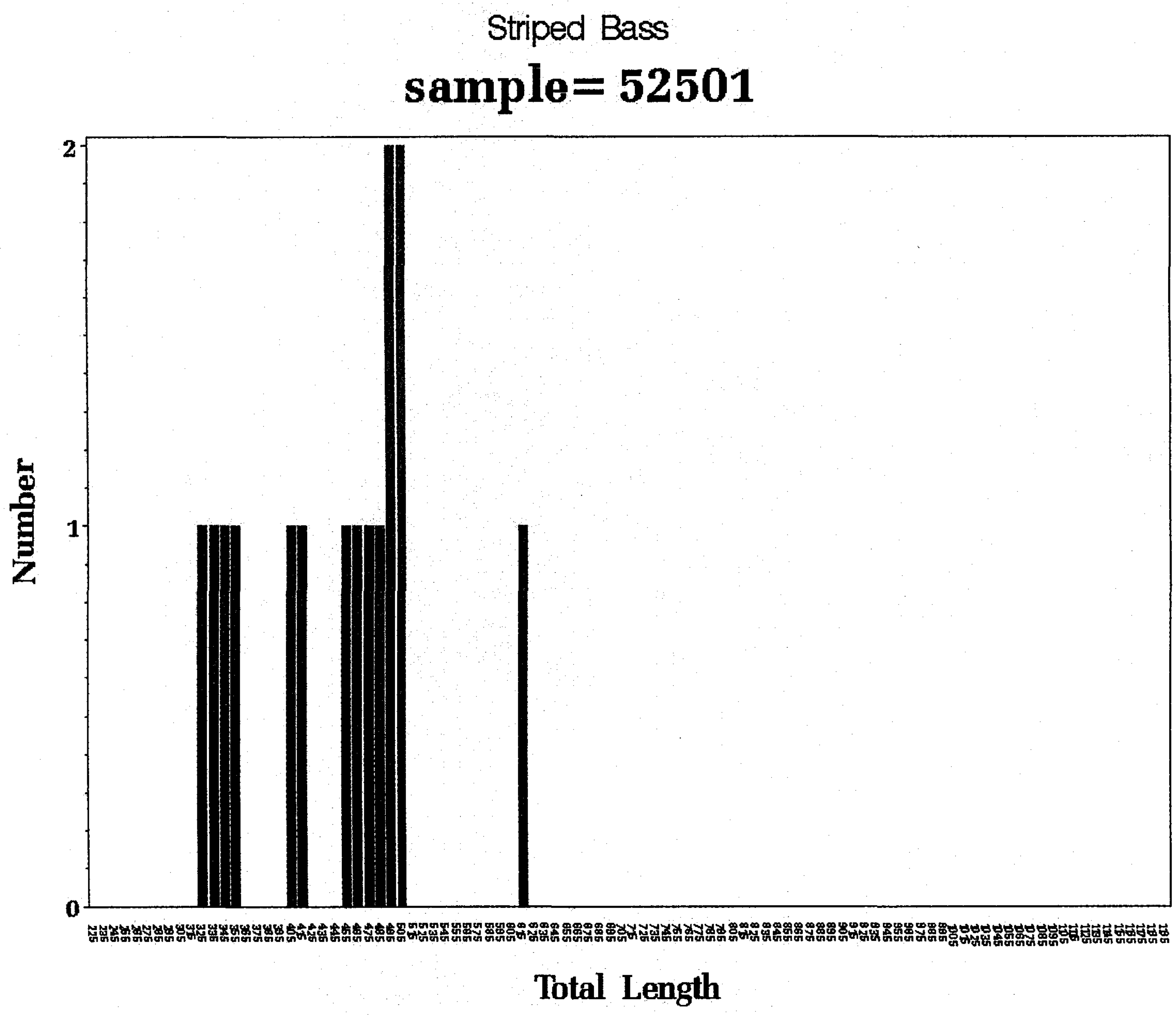

Gizzard Shad
sample=52501
Number
1
0
Total Length
290
295
300
305
310
315
320
325
330
335
340
345
350
355
360
365
370
375
380
385
390
395
400
405
410
415
420
425
430
435
440
445
450
455
460

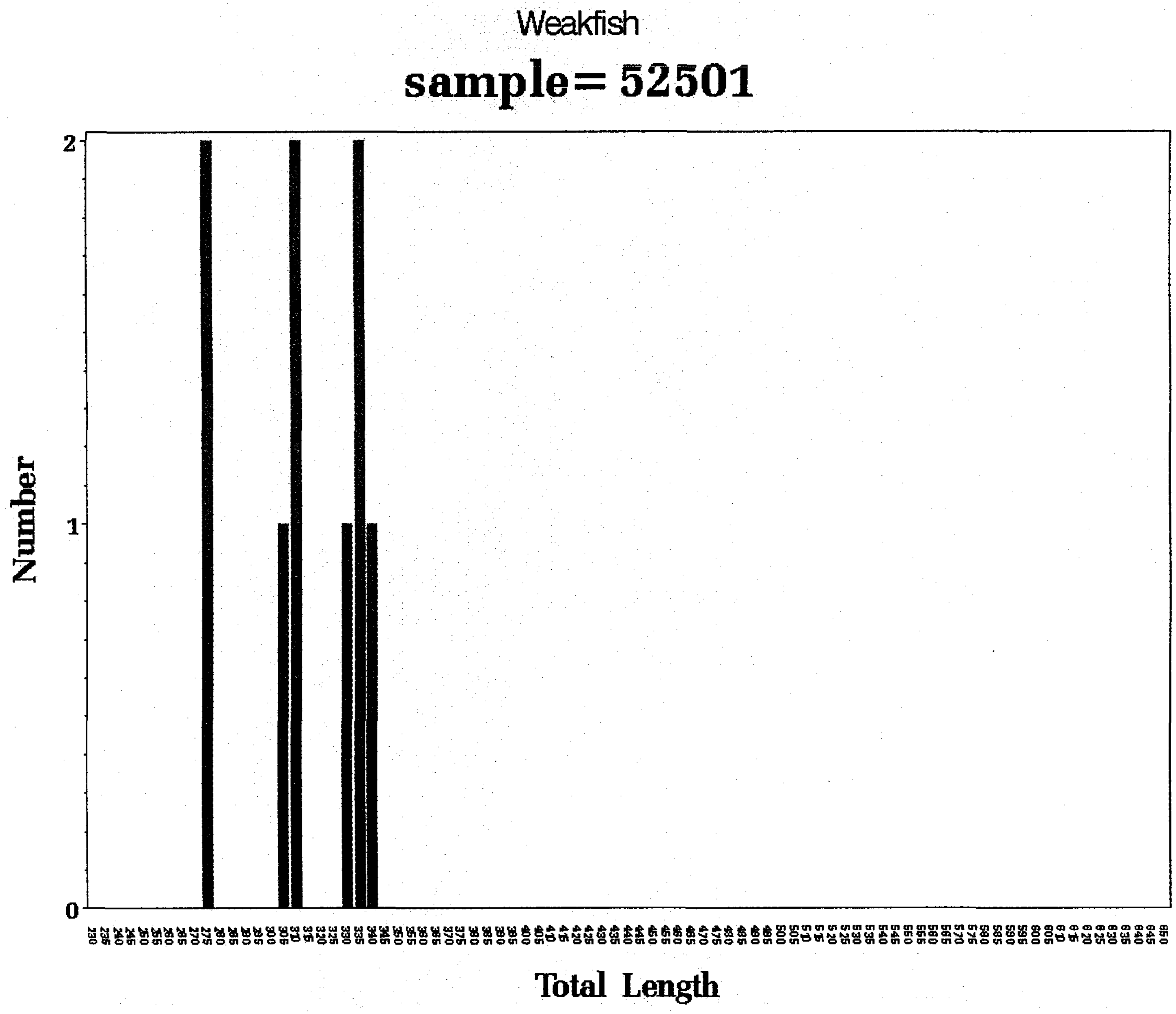

Spot
sample= 52501
Number
0
1
2
3
4
5
6
7
8
Total Length
125
130
135
140
145
150
155
160
165
170
175
180
185
190
195
200
205
210
215
220
225
230
235
240
245
250
255
260
265
270
275
280
285
290
295
300
305
310
315
320
325
330

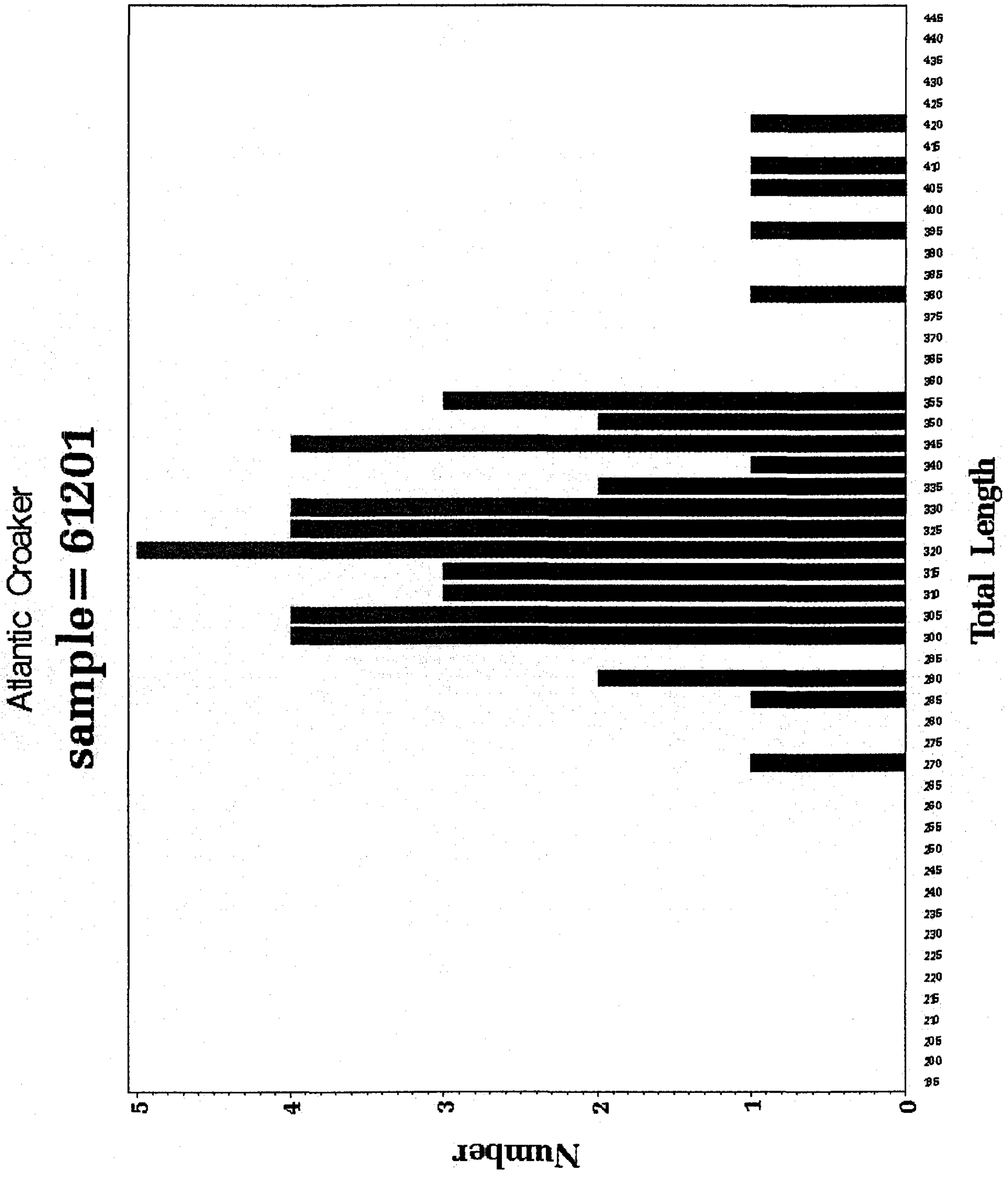
Bluefish

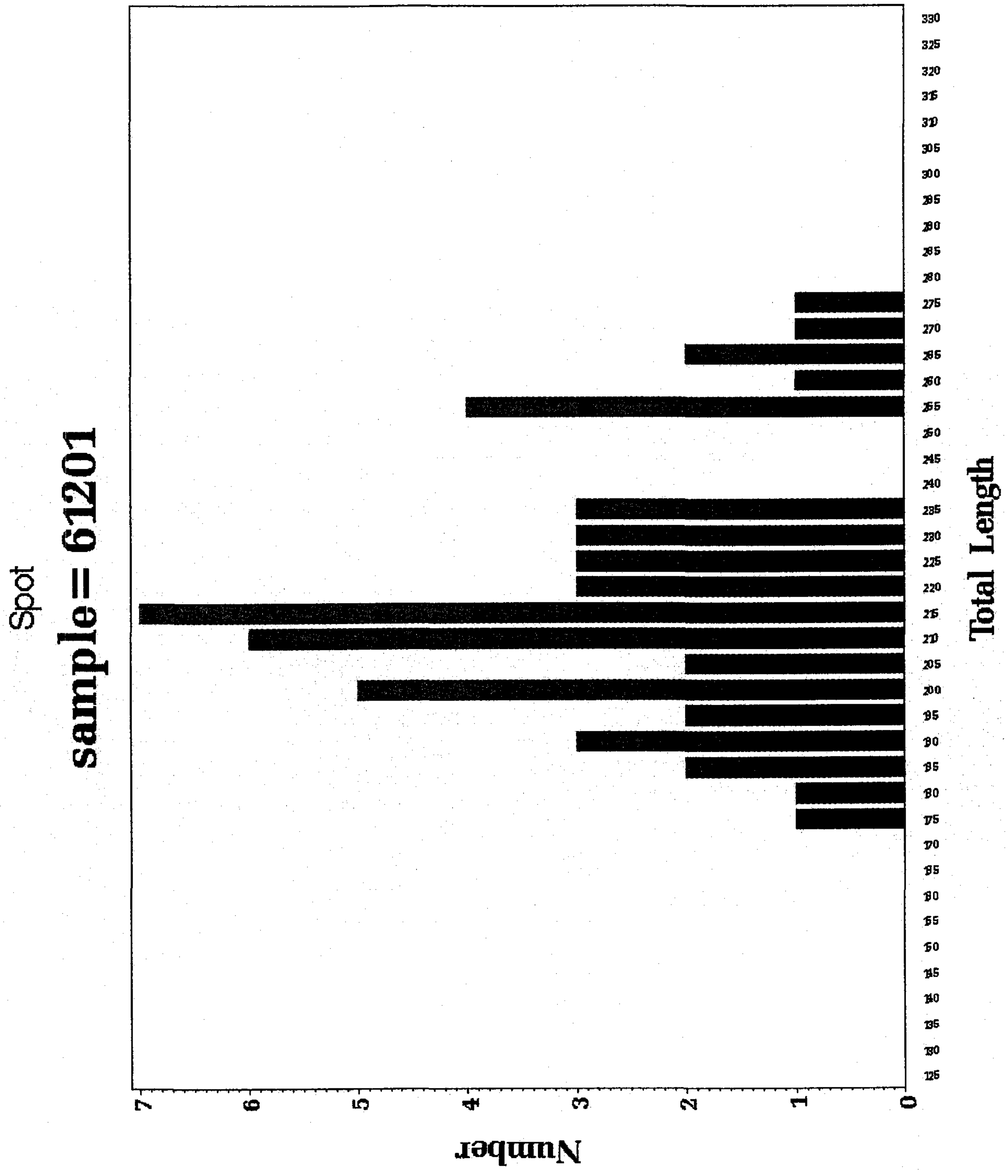
sample= 52501

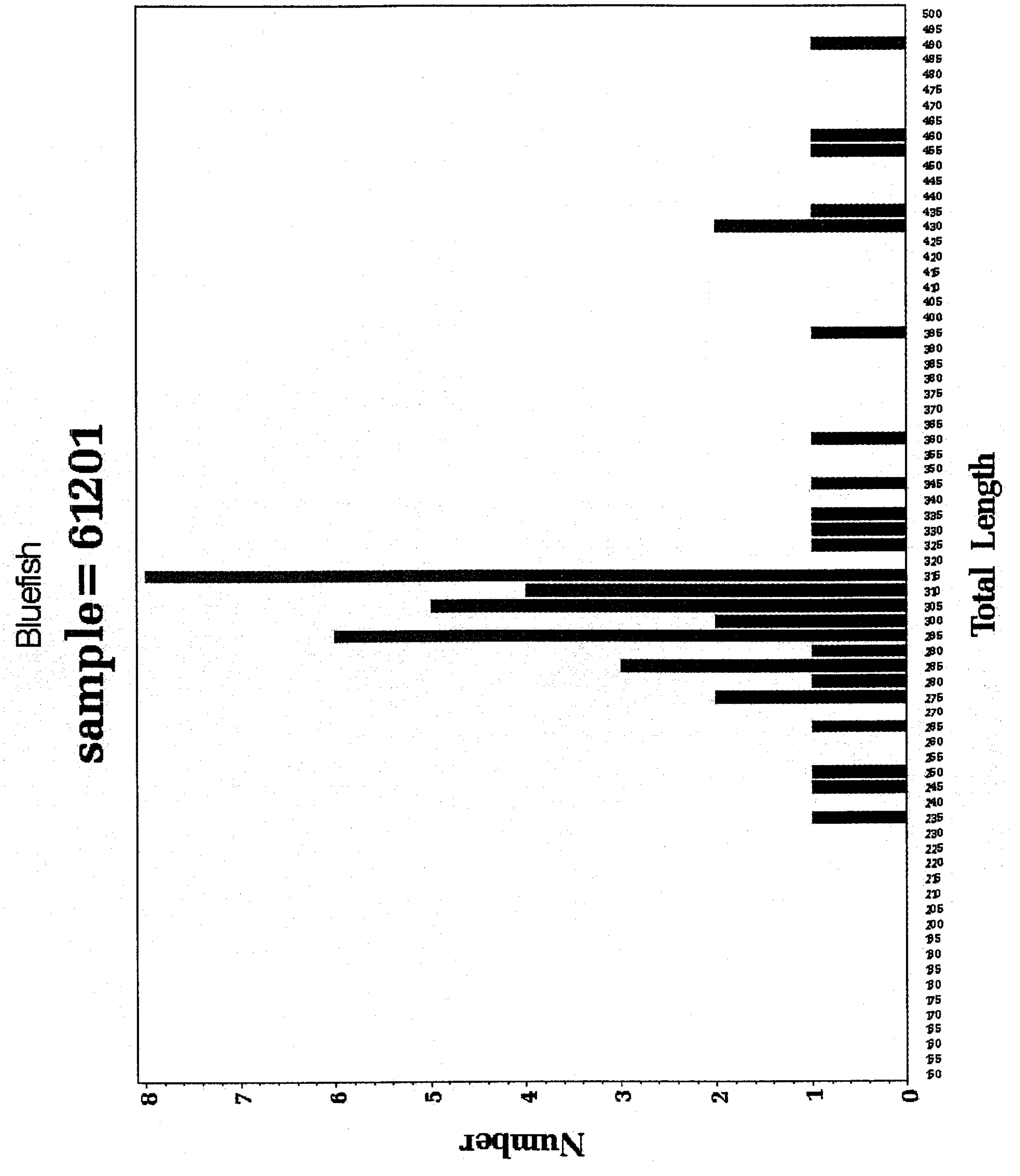


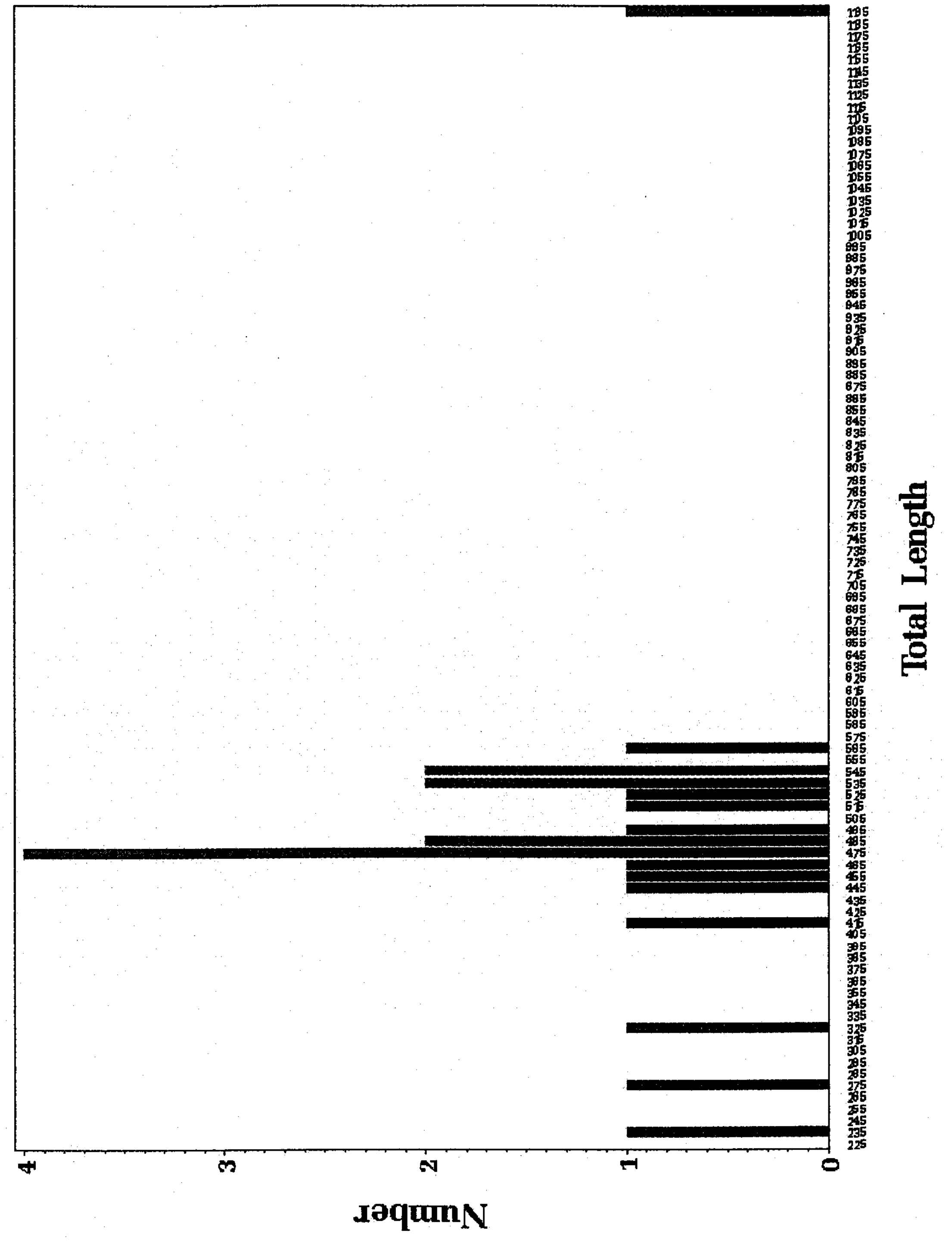

Striped Bass
sample= 52501
Number
2
1
0
225 235 245 255 265 275 285 295 305 315 325 335 345 355 365 375 385 395 405 415 425 435 445 455 465 475 485 495 505 515 525 535 545 555 565 575 585 595 605 615 625 635 645 655 665 675 685 695 705 715 725 735 745 755 765 775 785 795 805 815 825 835 845 855 865 875 885 895 905 915 925 935 945 955 965 975 985 995 1005 1015 1025 1035 1045 1055 1065 1075 1085 1095 1105 1115 1125 1135 1145 1155 1165 1175 1185 1195
Total Length


Weakfish
sample= 52501
Number
0
1
2
Total Length
230 235 240 245 250 255 260 265 270 275 280 285 290 295 300 305 310 315 320 325 330 335 340 345 350 355 360 365 370 375 380 385 390 395 400 405 410 415 420 425 430 435 440 445 450 455 460 465 470 475 480 485 490 495 500 505 510 515 520 525 530 535 540 545 550 555 560 565 570 575 580 585 590 595 600 605 610 615 620 625 630 635 640 645 650


Atlantic Croaker
sample = 61201
Number
0
1
2
3
4
5
Total Length
195
200
205
210
215
220
225
230
235
240
245
250
255
260
265
270
275
280
285
290
295
300
305
310
315
320
325
330
335
340
345
350
355
360
365
370
375
380
385
390
395
400
405
410
415
420
425
430
435
440
445

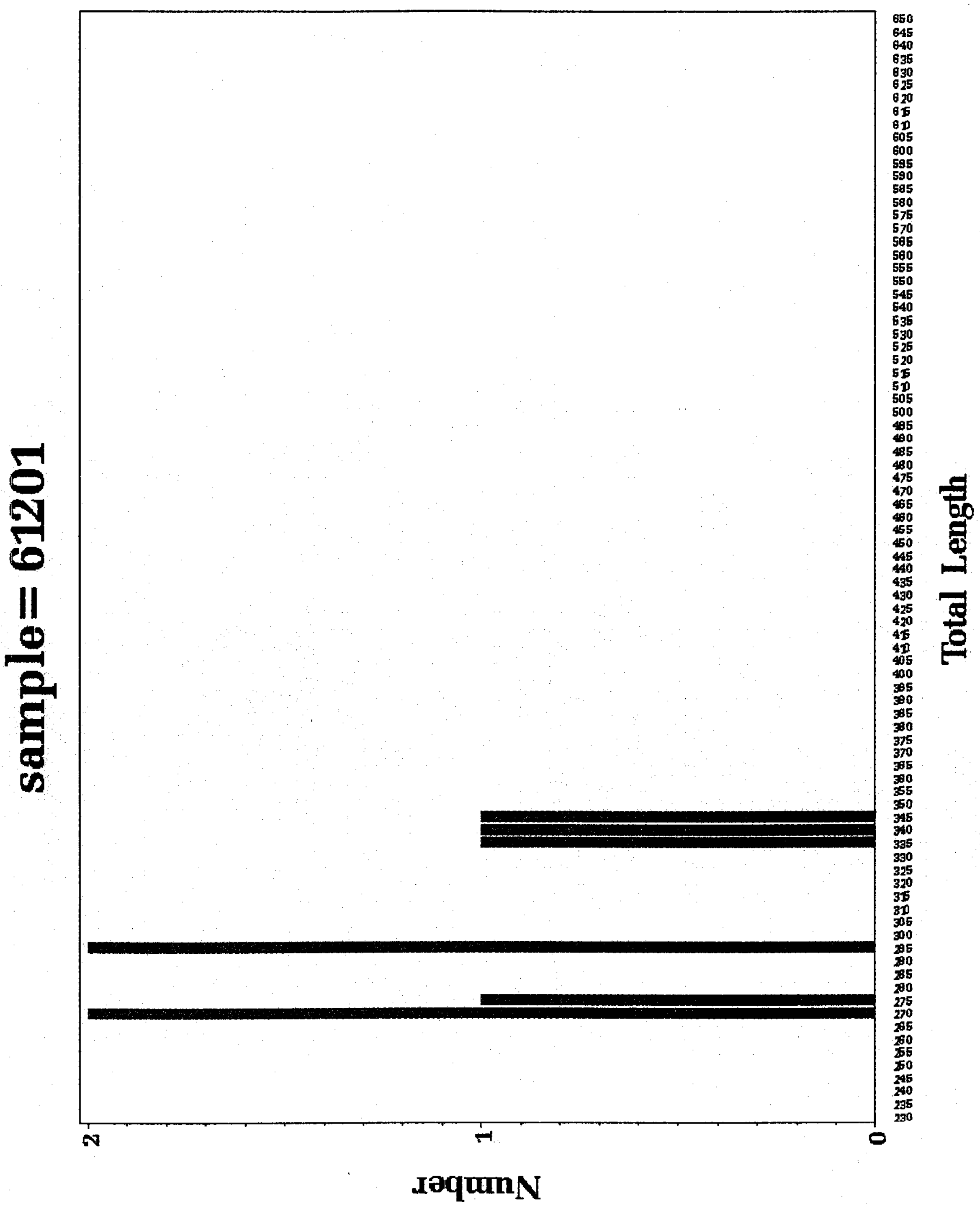

Spot
sample= 61201
Number
0
1
2
3
4
5
6
7
Total Length
125
130
135
140
145
150
155
160
165
170
175
180
185
190
195
200
205
210
215
220
225
230
235
240
245
250
255
260
265
270
275
280
285
290
295
300
305
310
315
320
325
330


Bluefish
sample= 61201
Number
0
1
2
3
4
5
6
7
8
Total Length
160
165
170
175
180
185
190
195
200
205
210
215
220
225
230
235
240
245
250
255
260
265
270
275
280
285
290
295
300
305
310
315
320
325
330
335
340
345
350
355
360
365
370
375
380
385
390
395
400
405
410
415
420
425
430
435
440
445
450
455
460
465
470
475
480
485
490
495
500



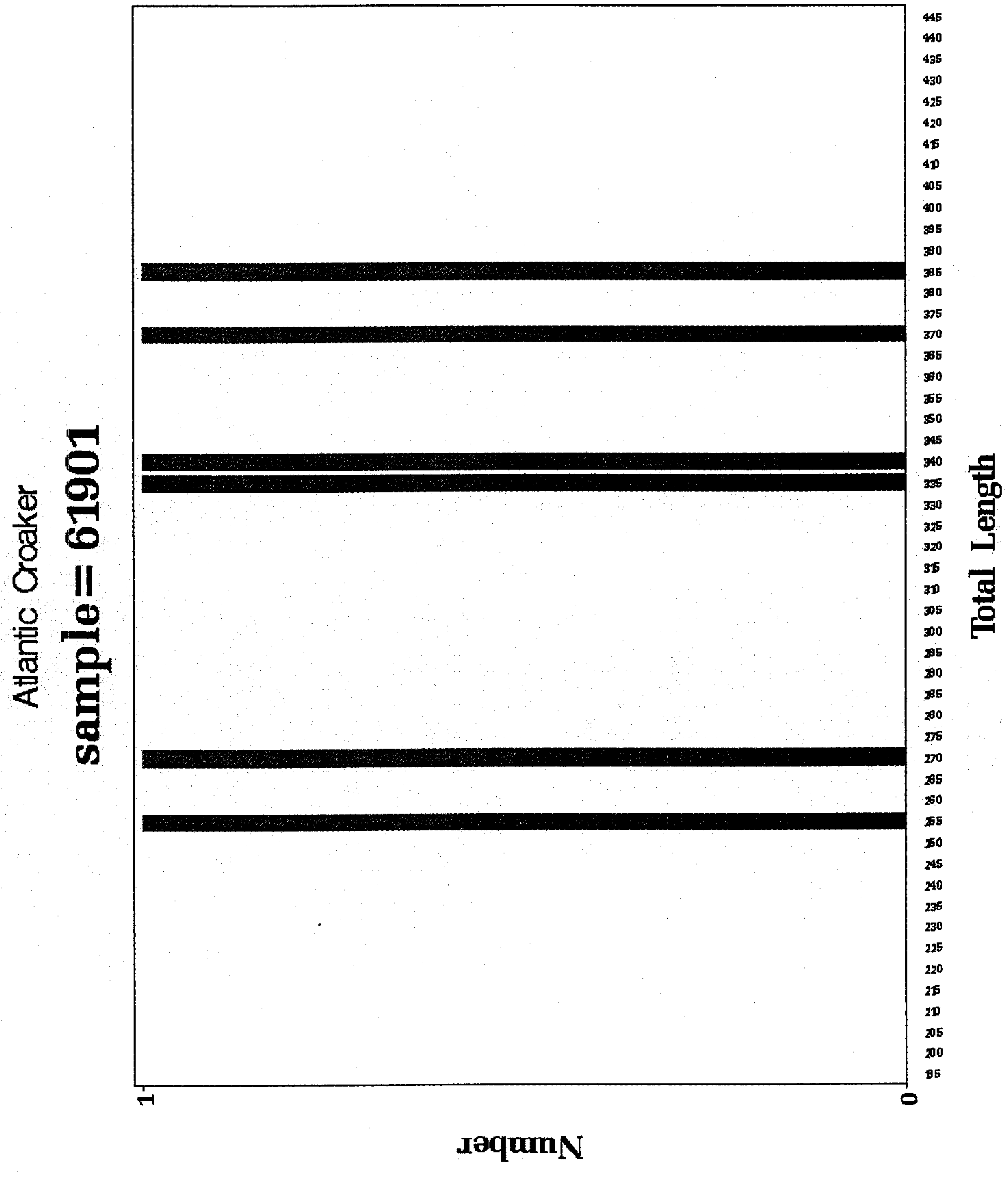
Striped Bass

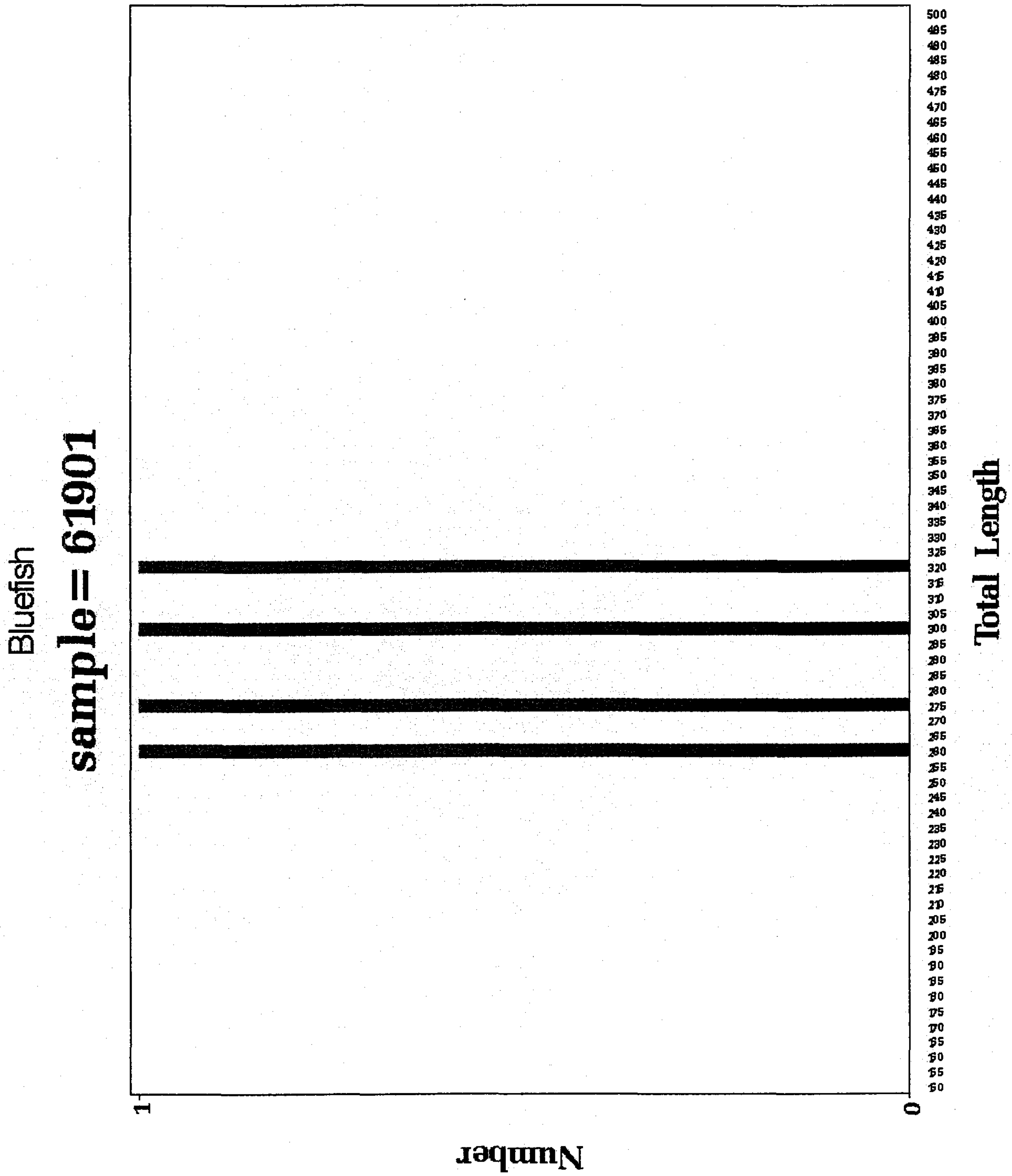
sample= 61201



Weakfish

sample= 61201


Atlantic Croaker
sample=61901
Total Length
Number
0
1
445
440
435
430
425
420
415
410
405
400
395
390
385
380
375
370
365
360
355
350
345
340
335
330
325
320
315
310
305
300
295
290
285
280
275
270
265
260
255
250
245
240
235
230
225
220
215
210
205
200
195


Bluefish
sample= 61901
Total Length
Number
0
1
500
495
490
485
480
475
470
465
460
455
450
445
440
435
430
425
420
415
410
405
400
395
390
385
380
375
370
365
360
355
350
345
340
335
330
325
320
315
310
305
300
295
290
285
280
275
270
265
260
255
250
245
240
235
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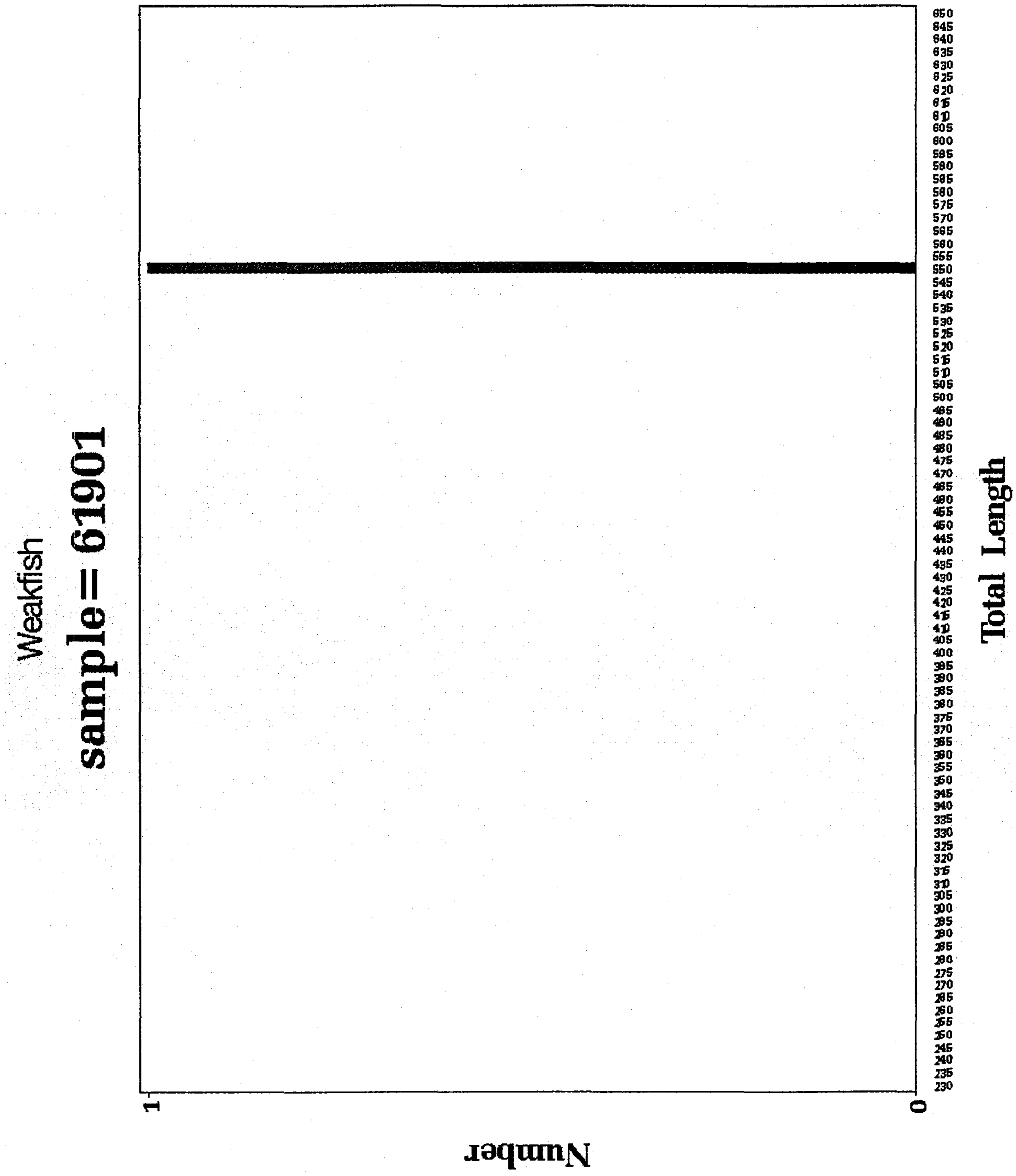
225
220
215
210
205
200
195
190
185
180
175
170
165
160
155
150


Weakfish
sample= 61901
Number
1
0
Total Length
230
235
240
245
250
255
260
265
270
275
280
285
290
295
300
305
310
315
320
325
330
335
340
345
350
355
360
365
370
375
380
385
390
395
400
405
410
415
420
425
430
435
440
445
450
455
460
465
470
475
480
485
490
495
500
505
510
515
520
525
530
535
540
545
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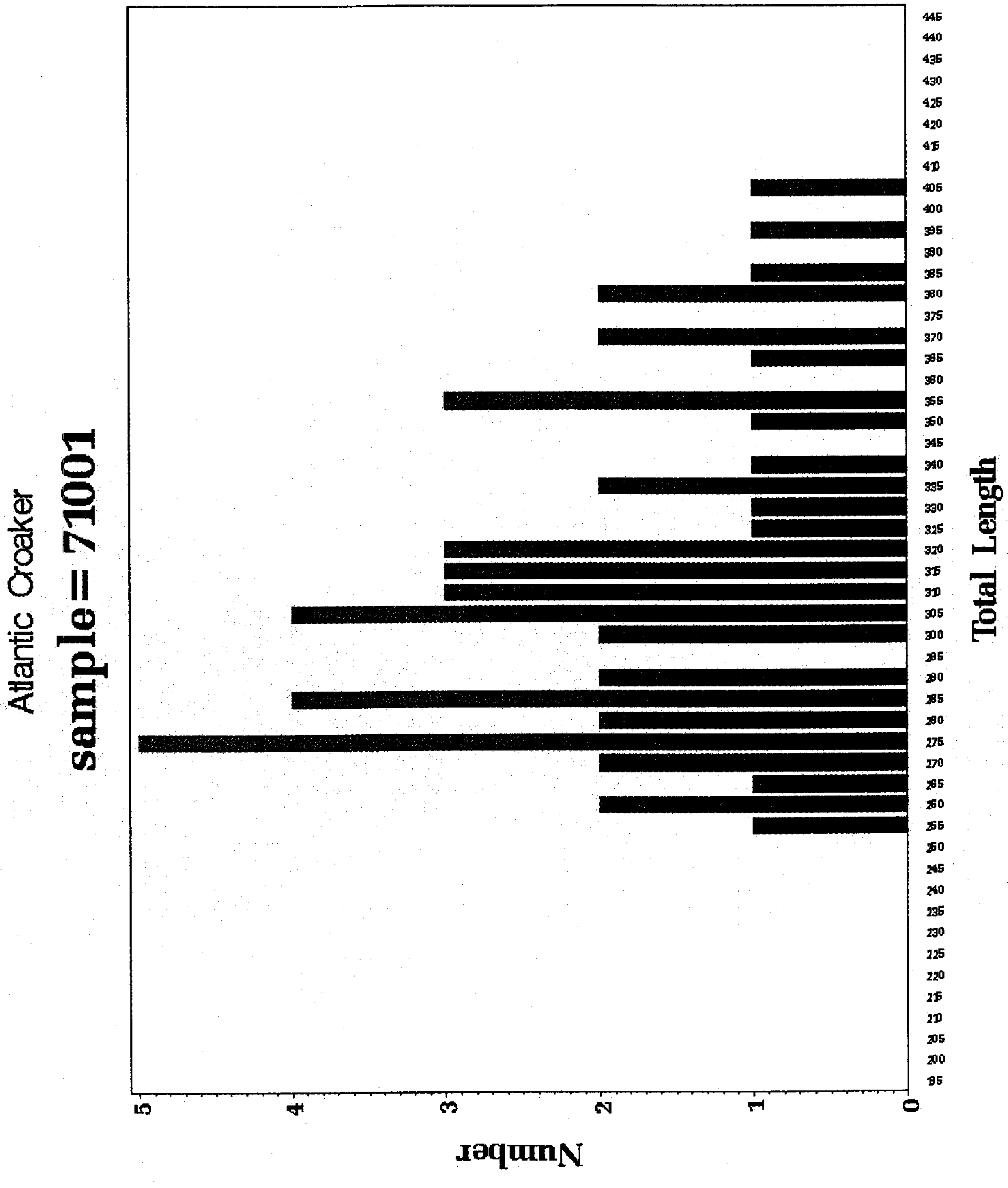
645
650

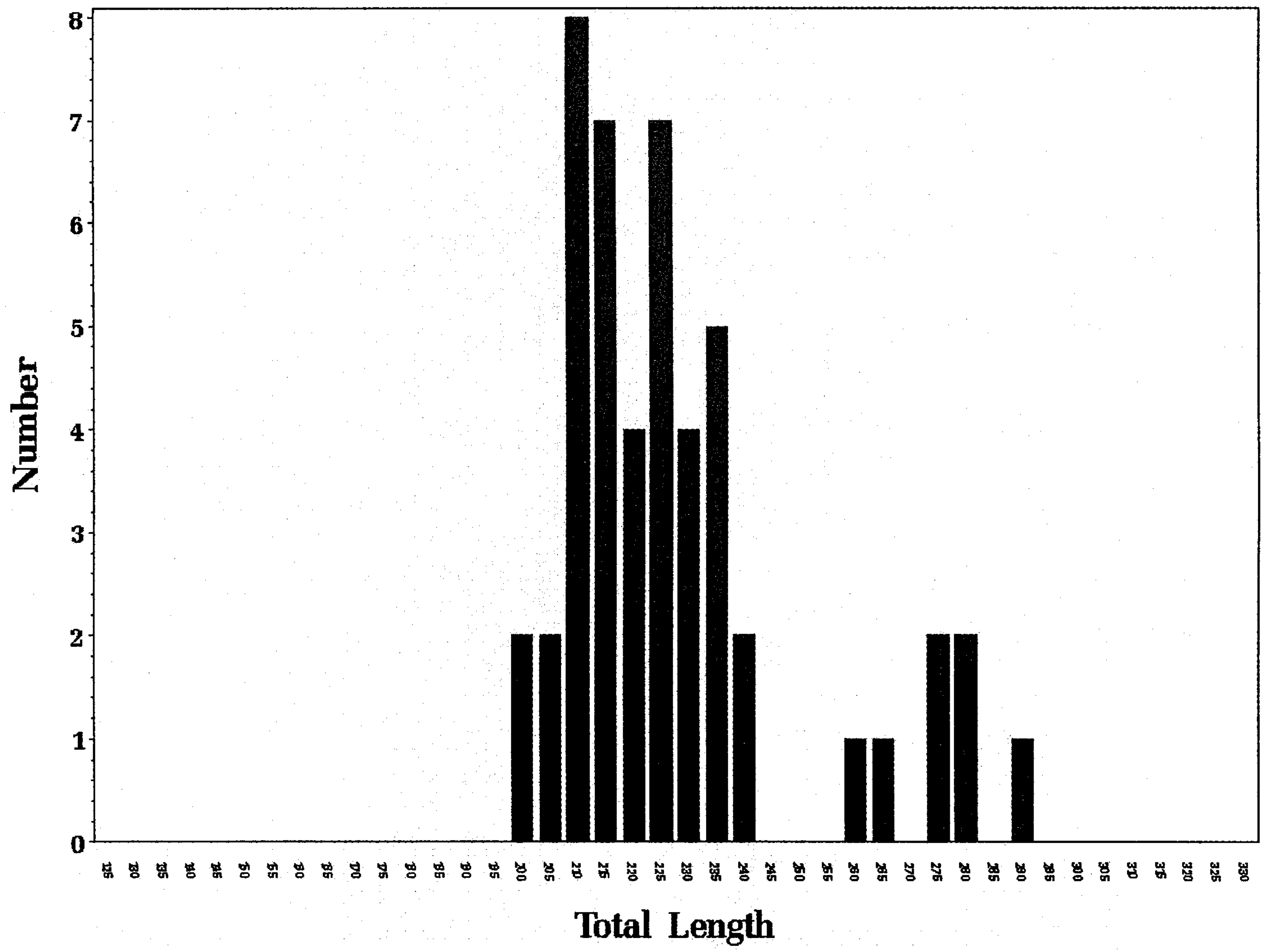


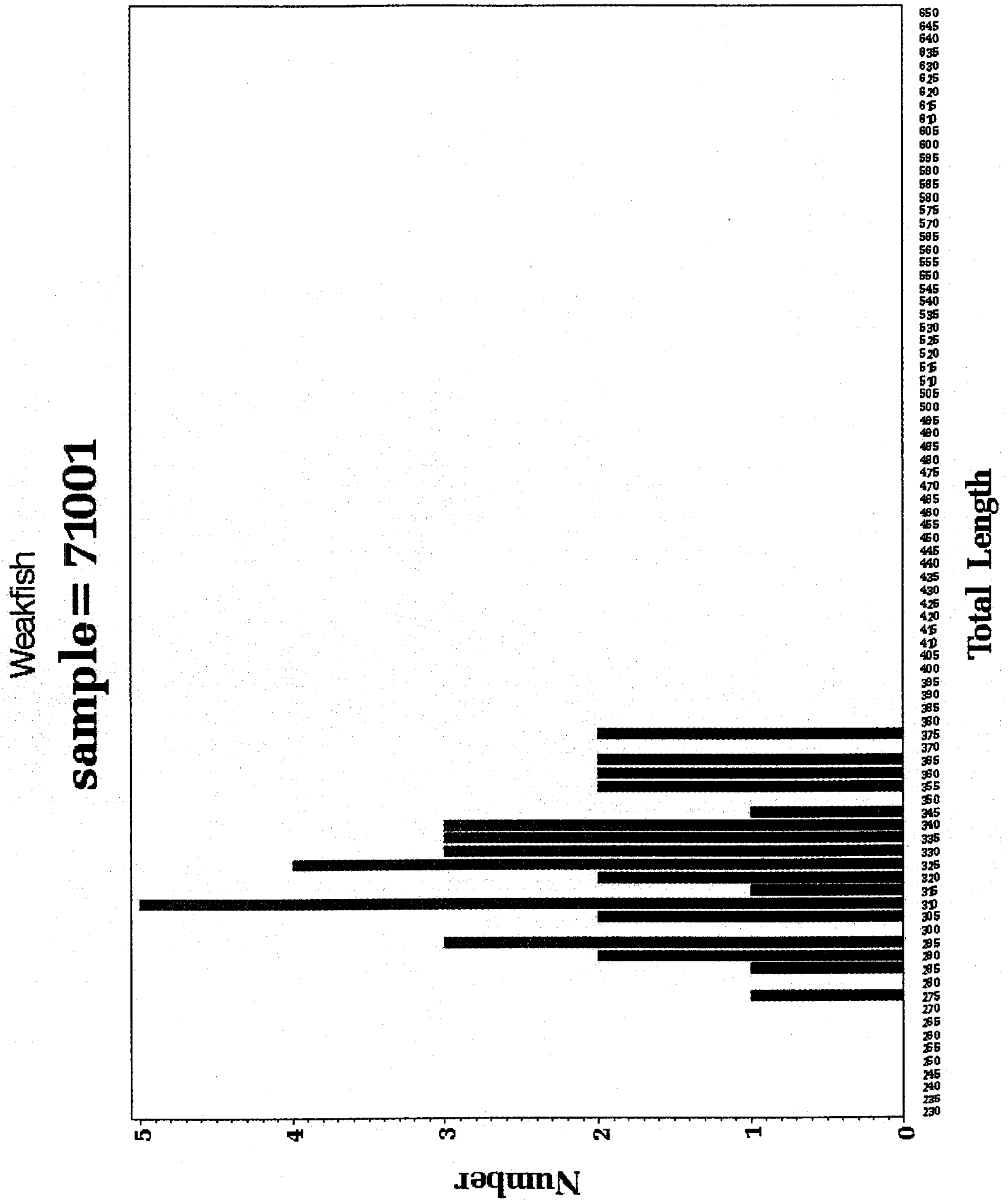
Atlantic Croaker

sample= 71001

Spot

sample= 71001




Weakfish
sample= 71001
Number
0
1
2
3
4
5
Total Length
230
235
240
245
250
255
260
265
270
275
280
285
290
295
300
305
310
315
320
325
330
335
340
345
350
355
360
365
370
375
380
385
390
395
400
405
410
415
420
425
430
435
440
445
450
455
460
465
470
475
480
485
490
495
500
505
510
515
520
525
530
535
540
545
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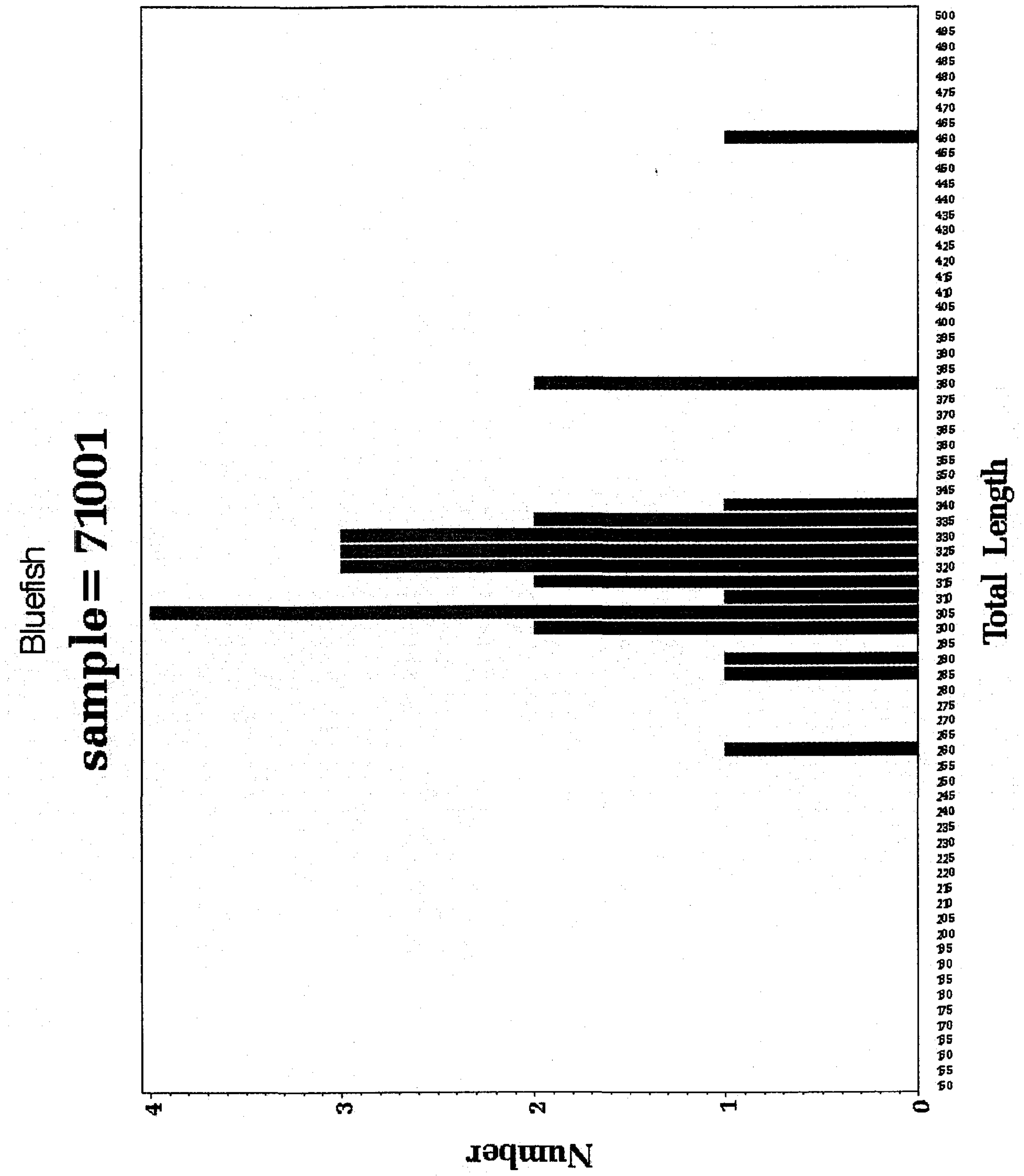
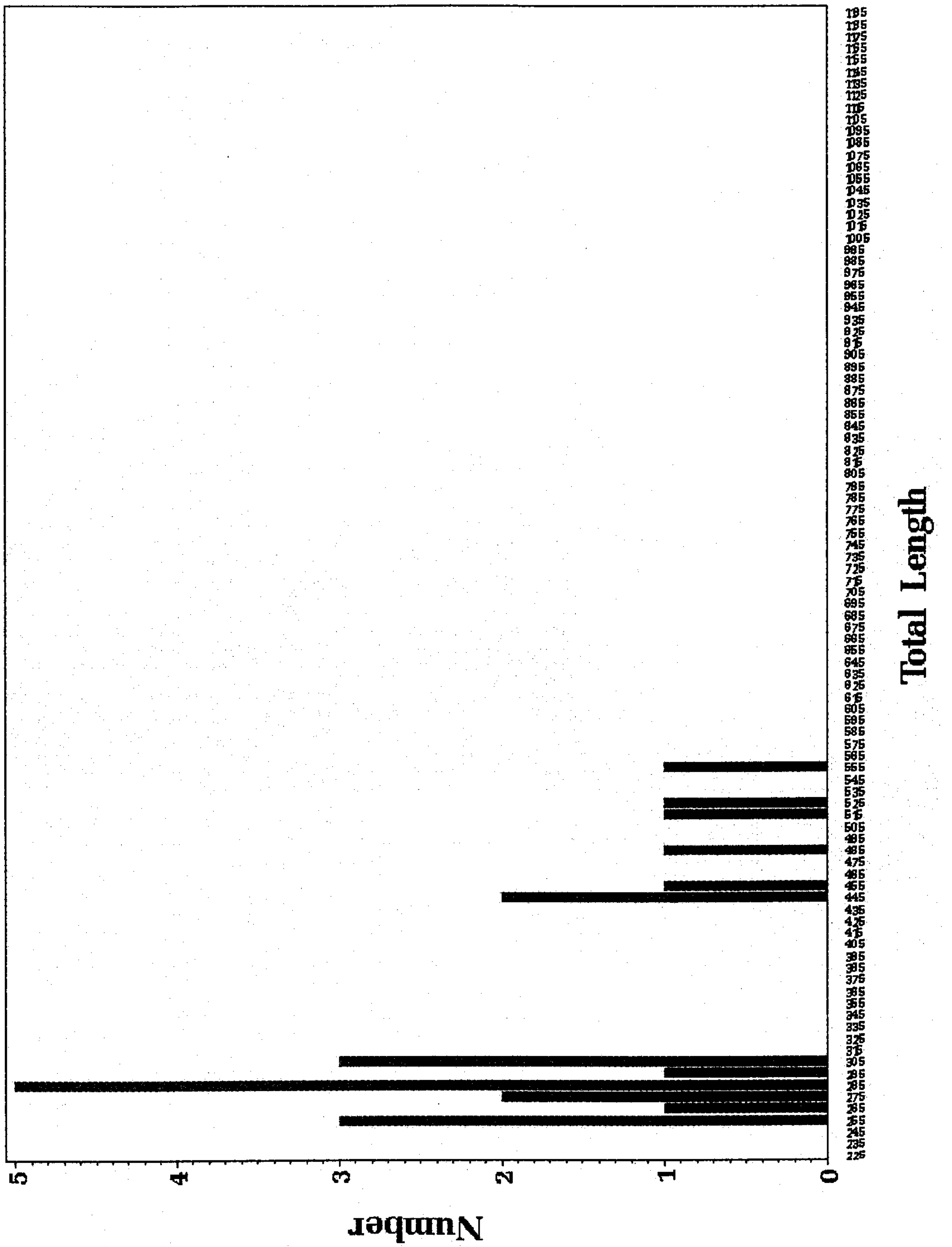
575
580
585
590
595
600
605
610
615
620
625
630
635
640
645
650

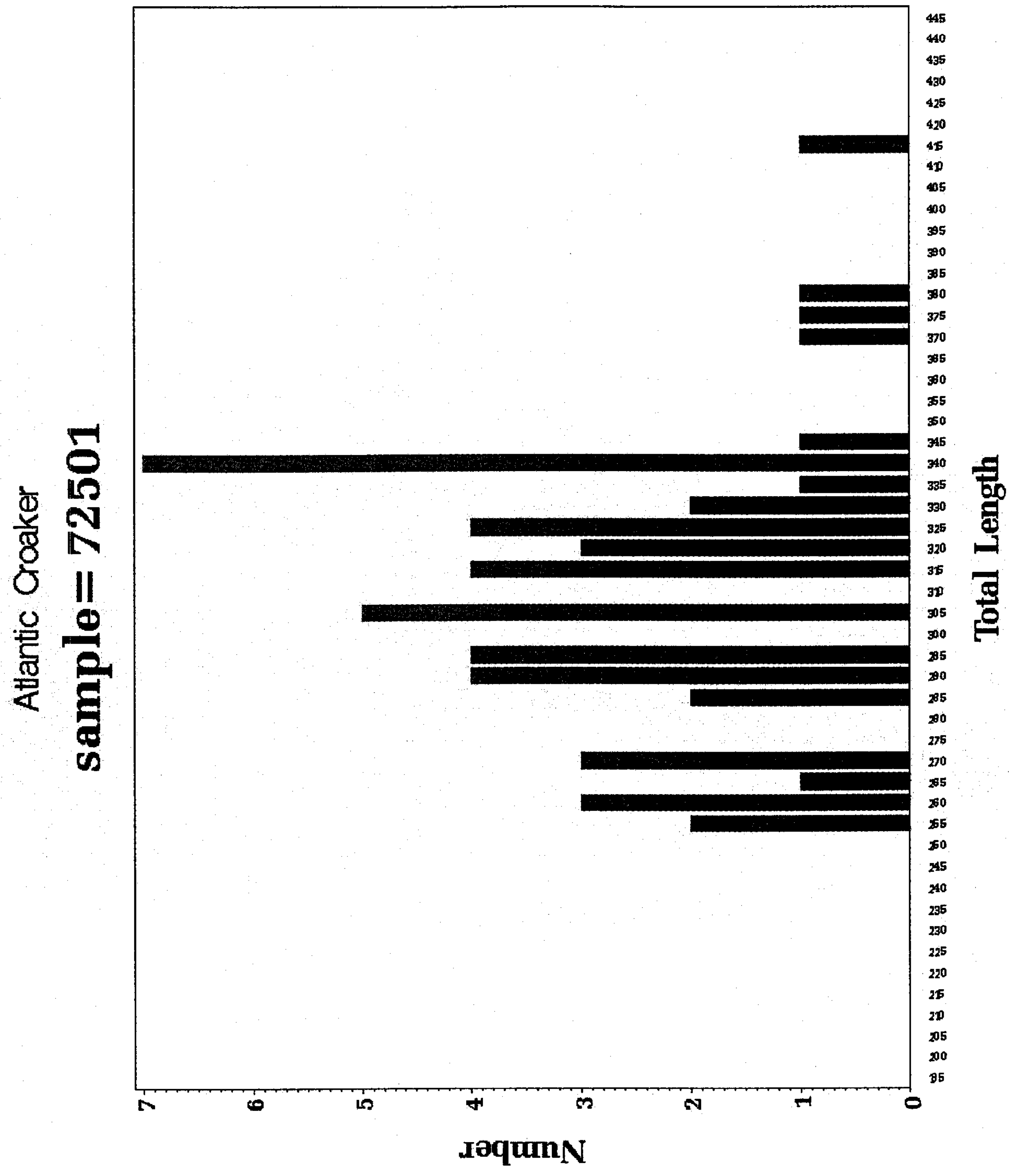

Bluefish

sample= 71001

Striped Bass

sample= 71001




Atlantic Croaker
sample= 72501
Number
0
1
2
3
4
5
6
7
Total Length
195
200
205
210
215
220
225
230
235
240
245
250
255
260
265
270
275
280
285
290
295
300
305
310
315
320
325
330
335
340
345
350
355
360
365
370
375
380
385
390
395
400
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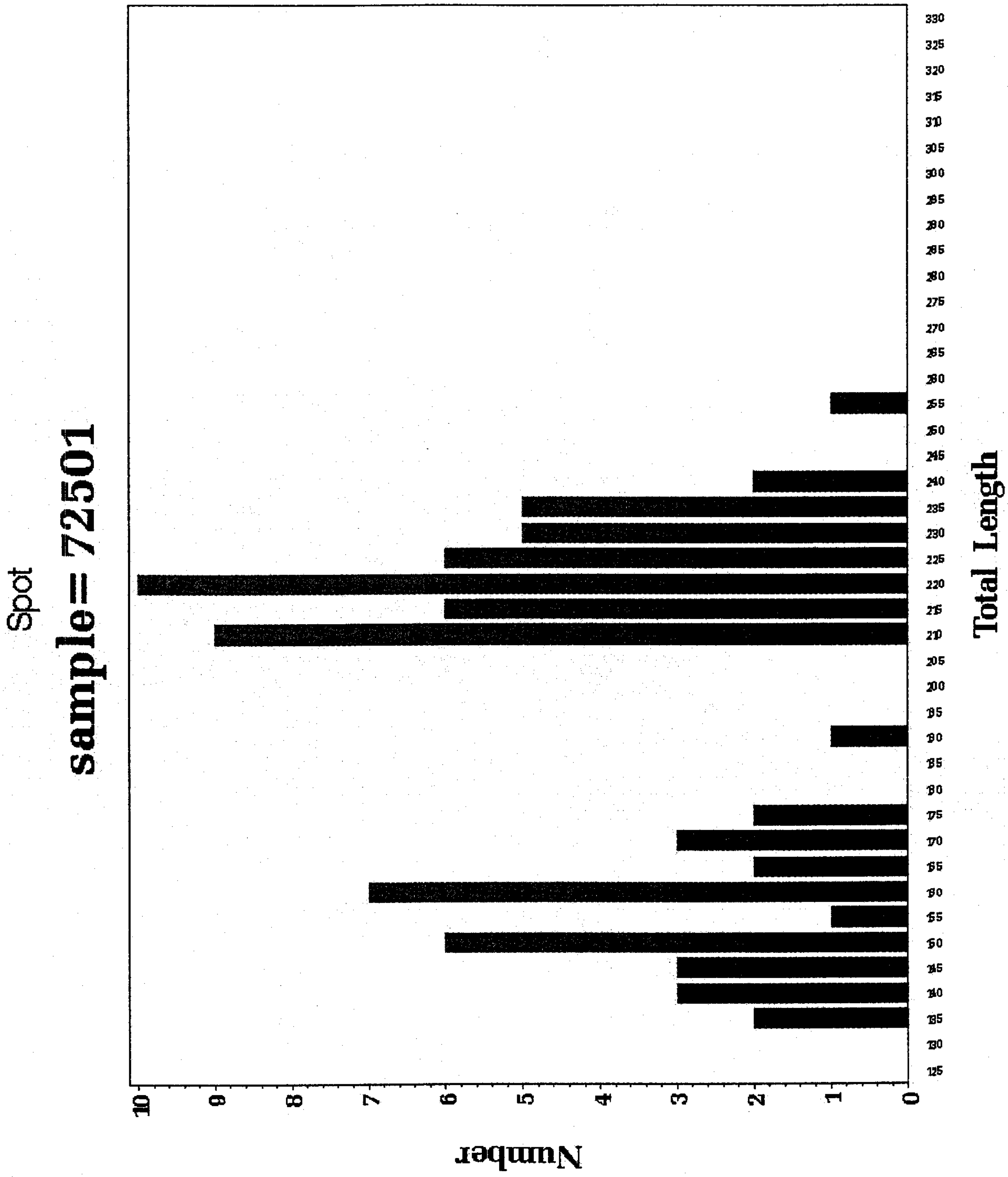
410
415
420
425
430
435
440
445


Spot
sample= 72501
Number
0
1
2
3
4
5
6
7
8
9
10
Total Length
125
130
135
140
145
150
155
160
165
170
175
180
185
190
195
200
205
210
215
220
225
230
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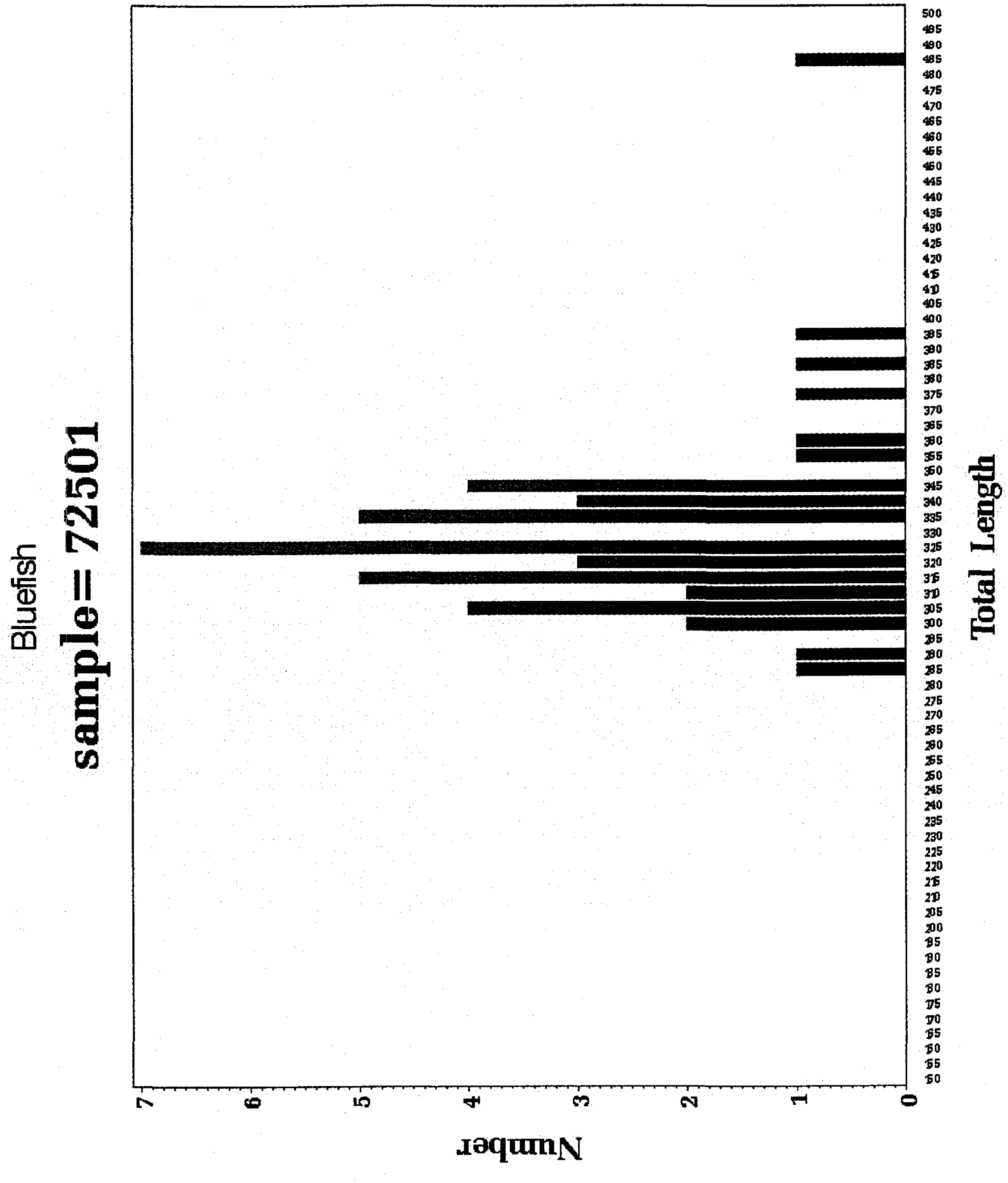
305
310
315
320
325
330


Bluefish
sample= 72501
Number
0
1
2
3
4
5
6
7
Total Length
150
155
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310
315
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325
330
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395
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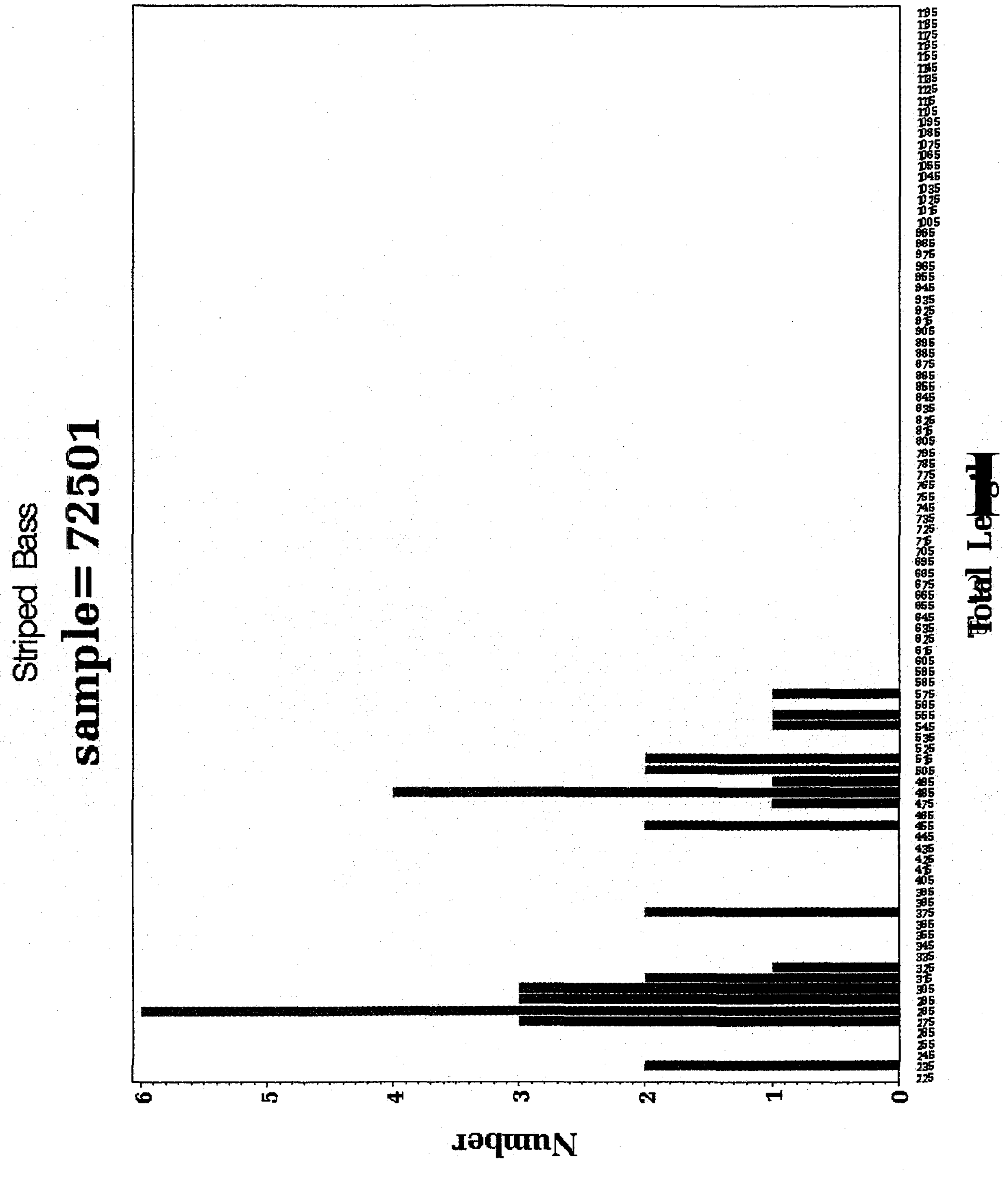
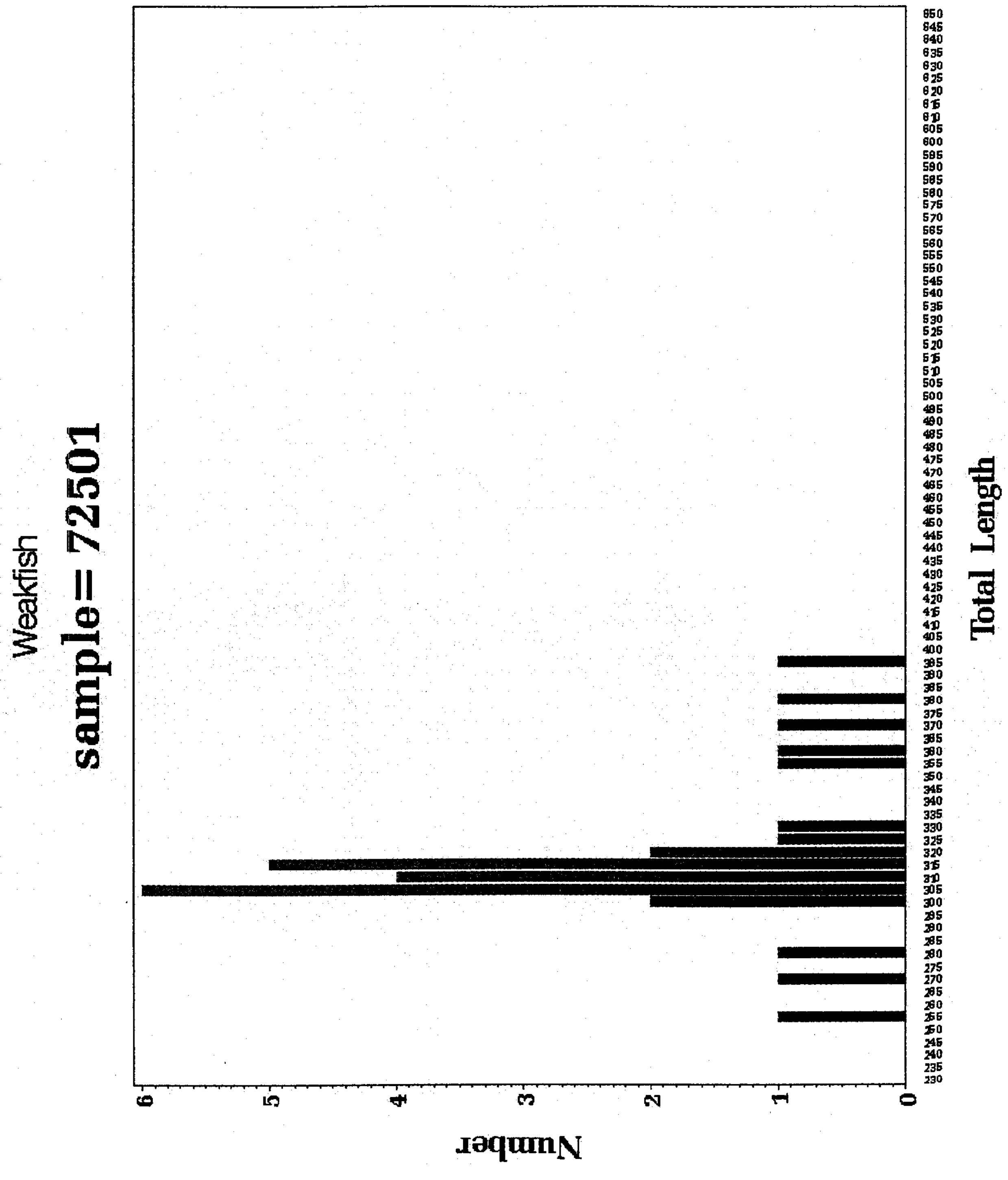
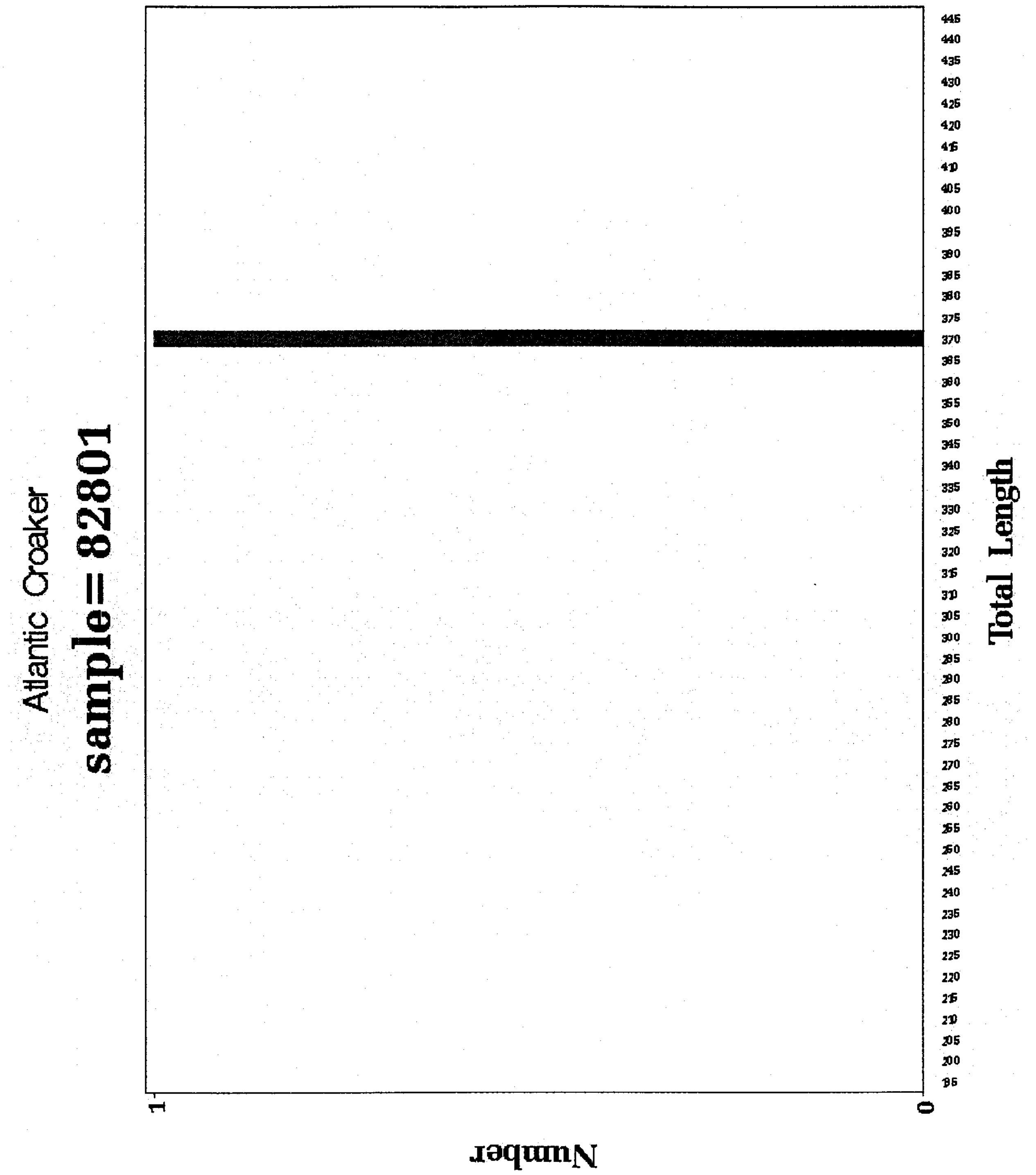


Striped Bass

sample= 72501


Weakfish
sample= 72501
Number
0
1
2
3
4
5
6
Total Length
230 235 240 245 250 255 260 265 270 275 280 285 290 295 300 305 310 315 320 325 330 335 340 345 350 355 360 365 370 375 380 385 390 395 400 405 410 415 420 425 430 435 440 445 450 455 460 465 470 475 480 485 490 495 500 505 510 515 520 525 530 535 540 545 550 555 560 565 570 575 580 585 590 595 600 605 610 615 620 625 630 635 640 645 650


Atlantic Croaker
sample= 82801
Total Length
Number
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1
195
200
205
210
215
220
225
230
235
240
245
250
255
260
265
270
275
280
285
290
295
300
305
310
315
320
325
330
335
340
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420
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430
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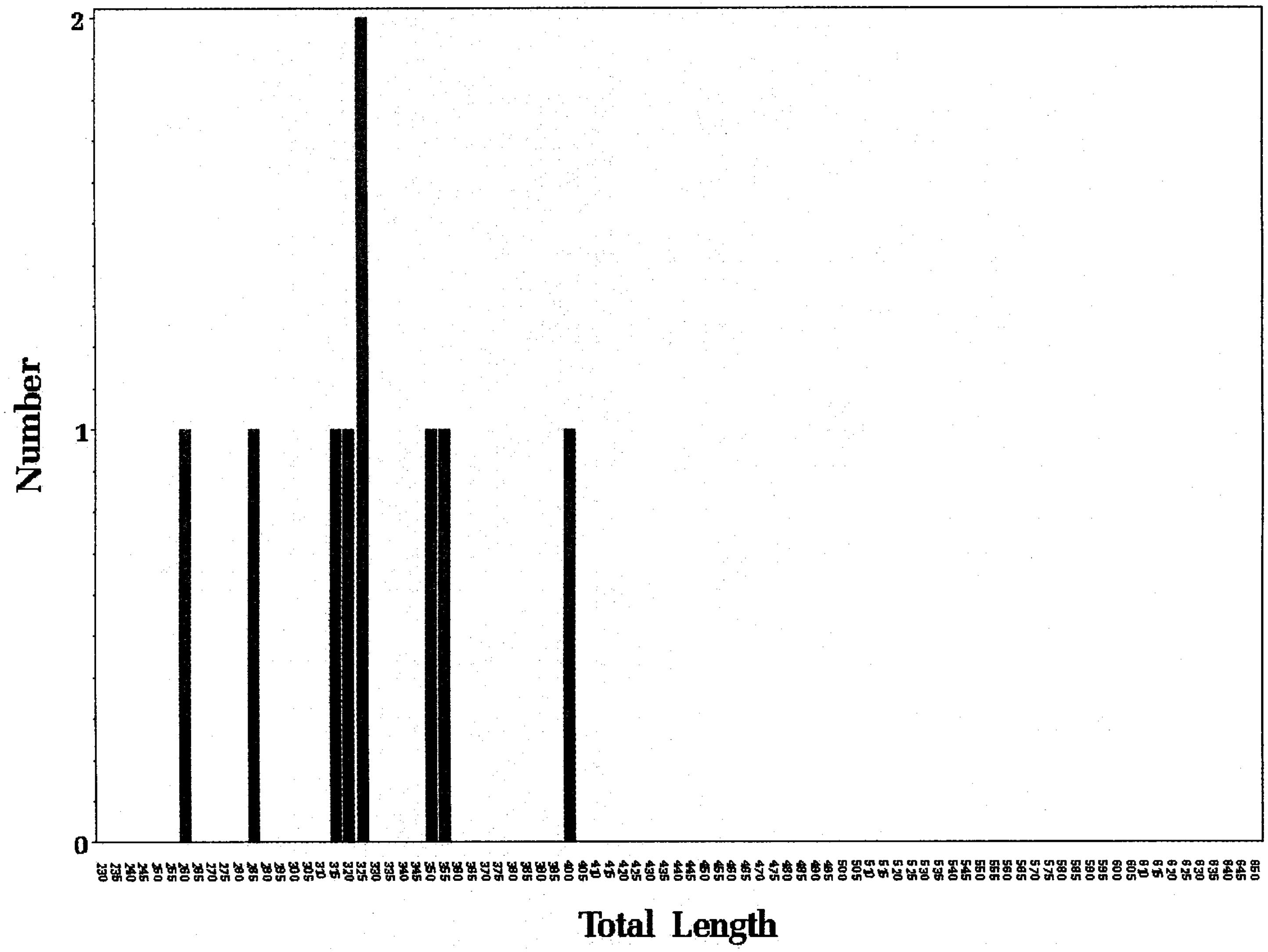
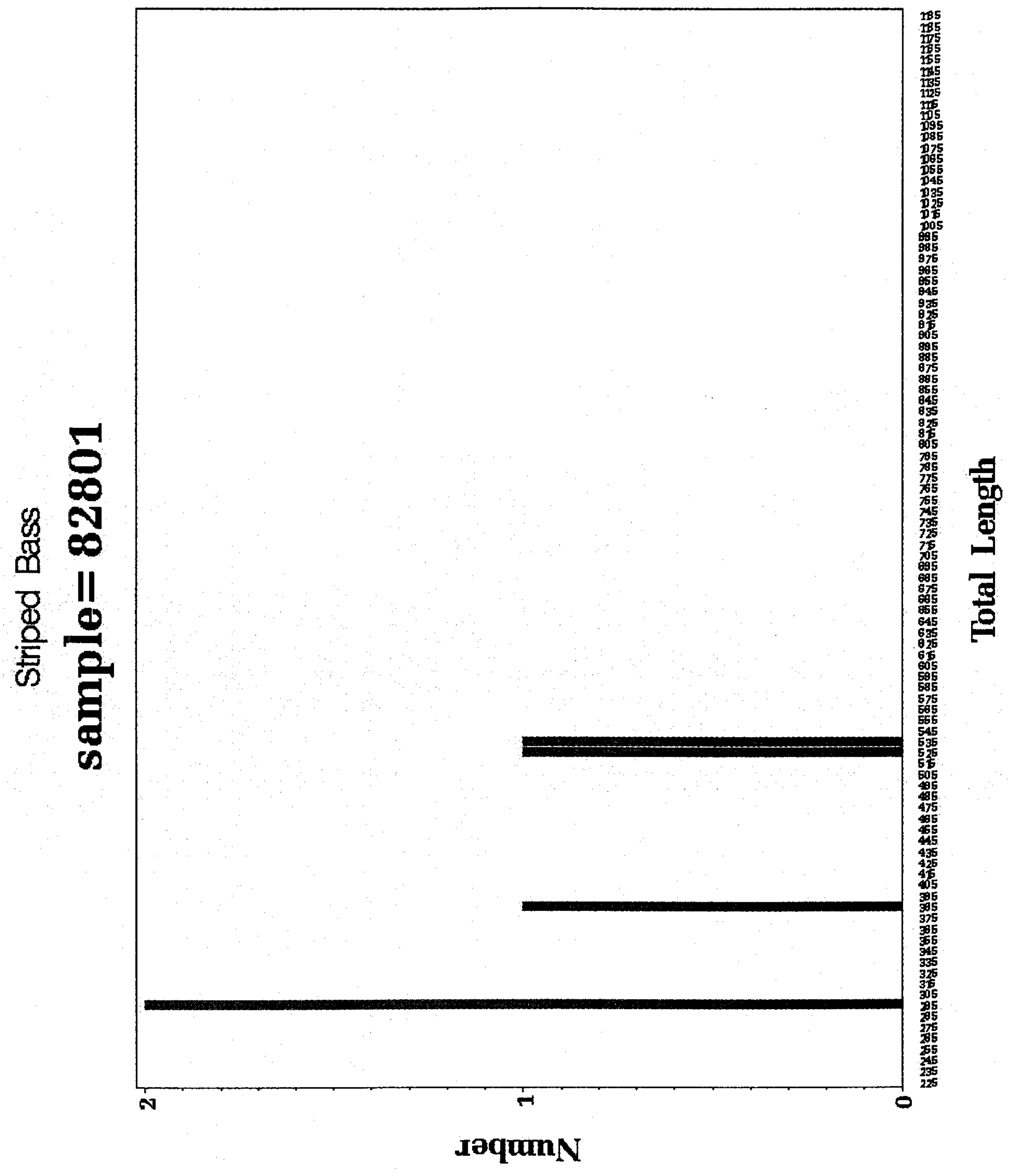
440
445



Weakfish

sample= 82801


Striped Bass
sample= 82801
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2
Total Length
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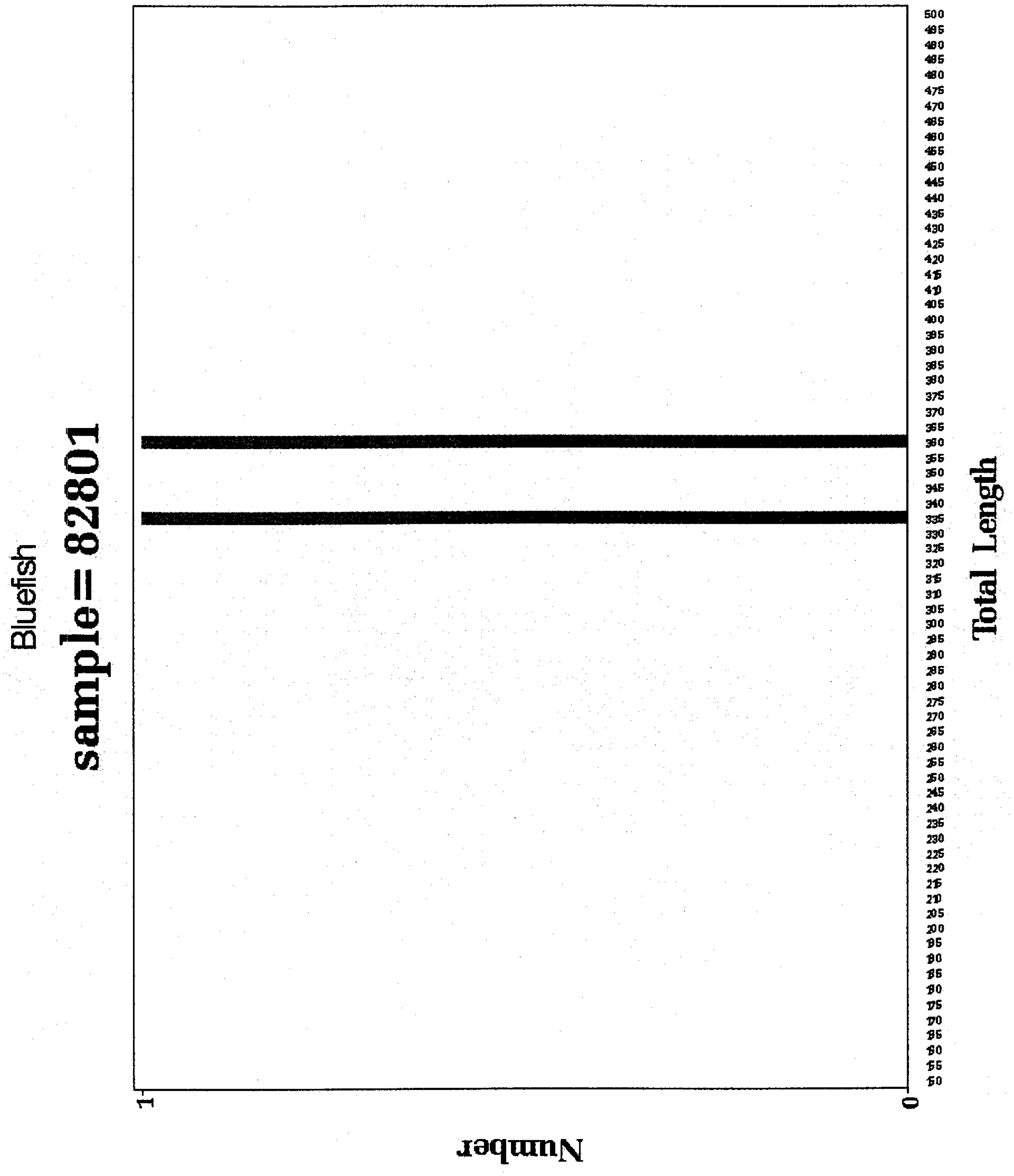
1185


Bluefish
sample= 82801
Total Length
Number
0
1
500
495
490
485
480
475
470
465
460
455
450
445
440
435
430
425
420
415
410
405
400
395
390
385
380
375
370
365
360
355
350
345
340
335
330
325
320
315
310
305
300
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255
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225
220
215
210
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200
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185
180
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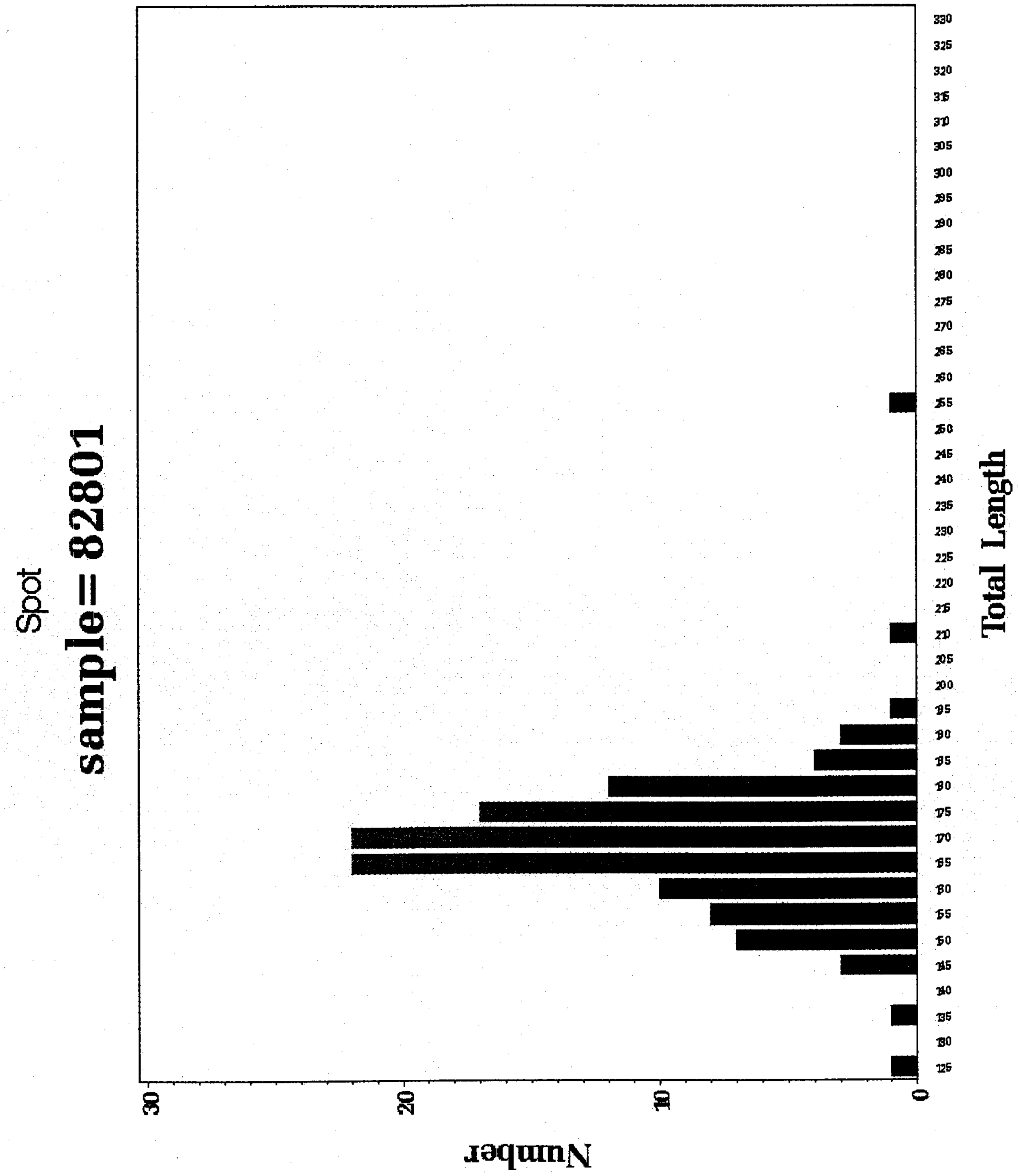
165
160
155
150


Spot
sample= 82801
Total Length
Number
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10
20
30
125
130
135
140
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150
155
160
165
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175
180
185
190
195
200
205
210
215
220
225
230
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240
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255
260
265
270
275
280
285
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295
300
305
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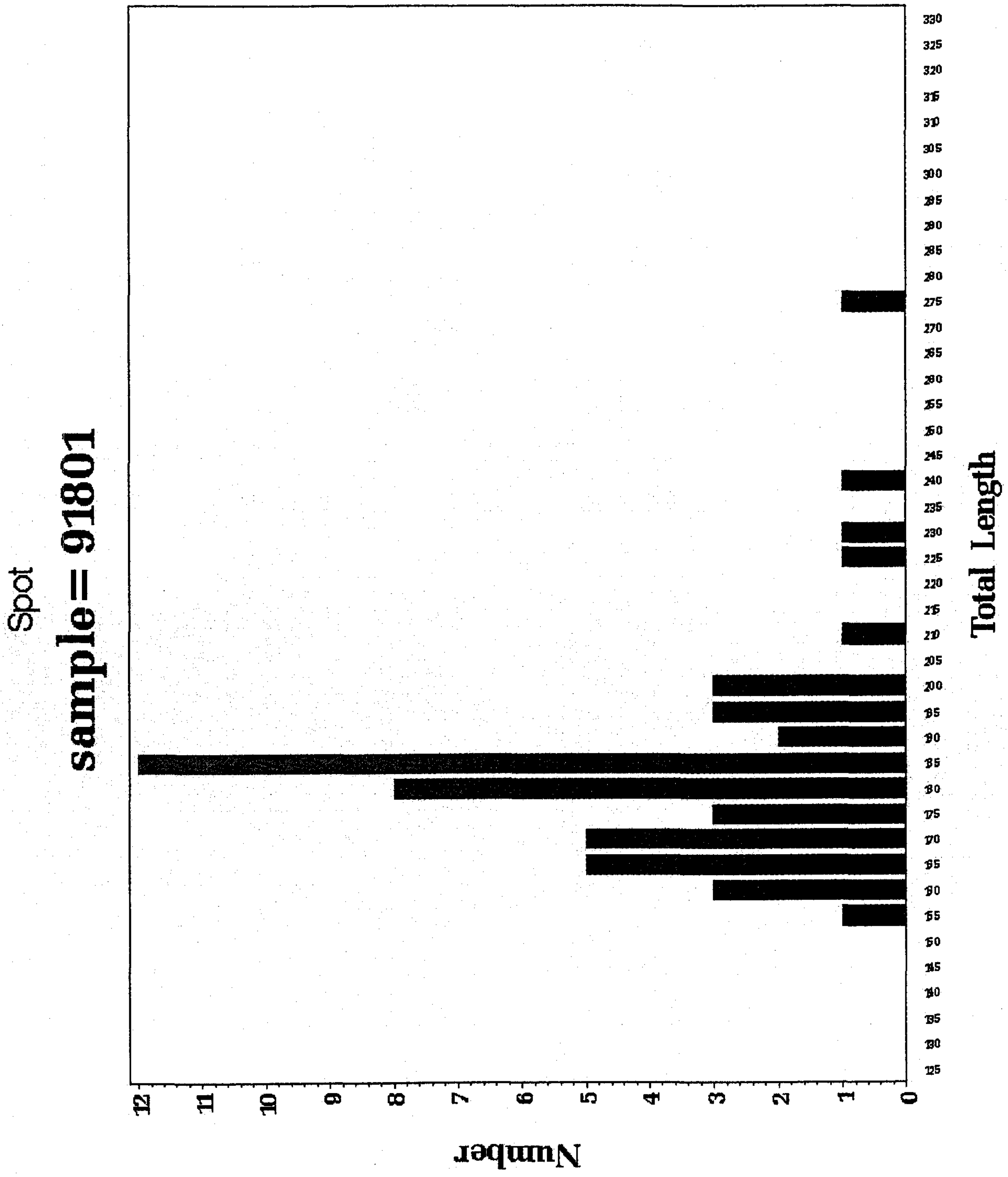
315
320
325
330


Spot
sample=91801
Number
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1
2
3
4
5
6
7
8
9
10
11
12
Total Length
125
130
135
140
145
150
155
160
165
170
175
180
185
190
195
200
205
210
215
220
225
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255
260
265
270
275
280
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295
300
305
310
315
320
325
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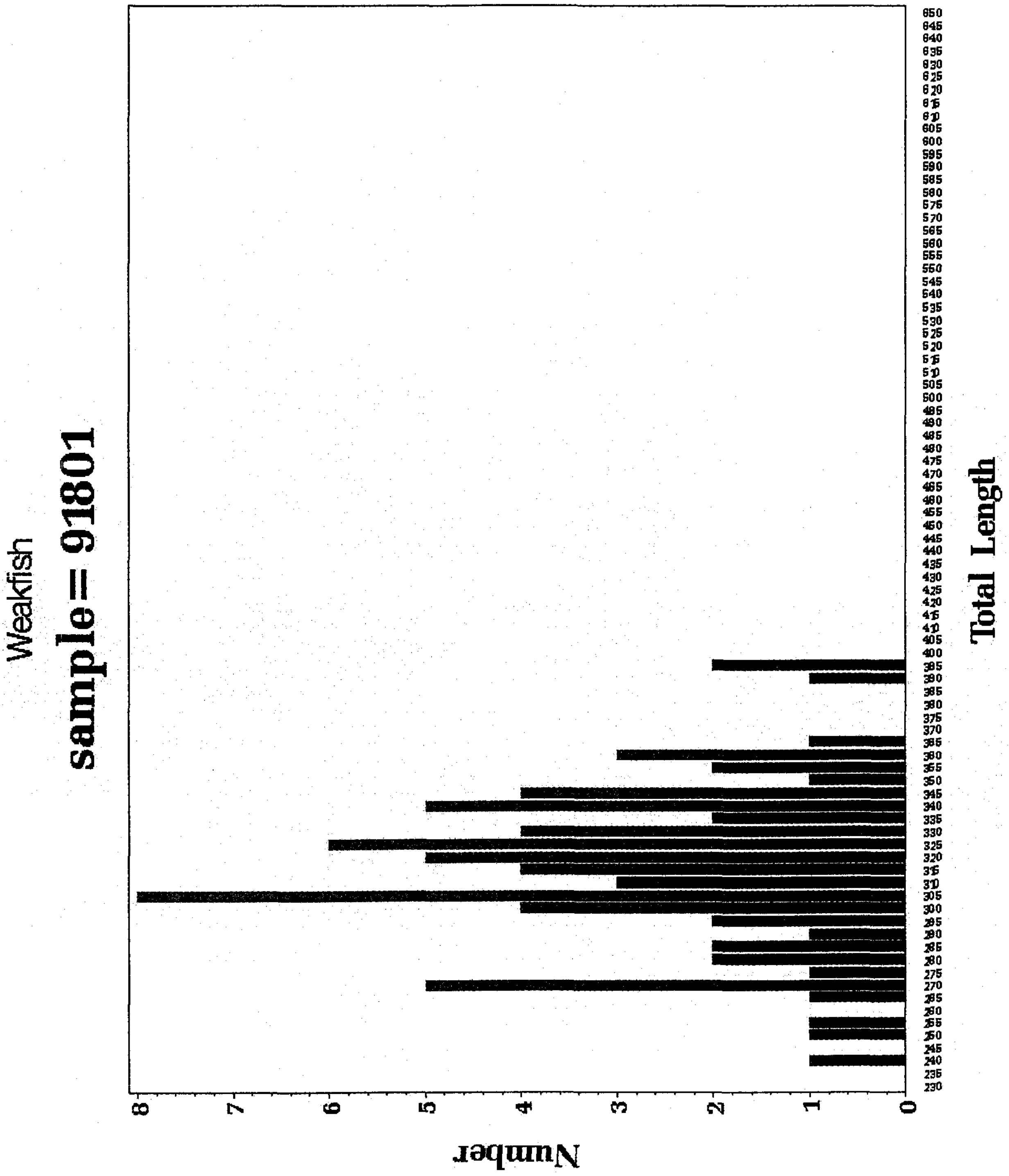
Weakfish
sample= 91801
Number
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1
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4
5
6
7
8
Total Length
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235
240
245
250
255
260
265
270
275
280
285
290
295
300
305
310
315
320
325
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335
340
345
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410
415
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425
430
435
440
445
450
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460
465
470
475
480
485
490
495
500
505
510
515
520
525
530
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540
545
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575
580
585
590
595
600
605
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615
620
625
630
635
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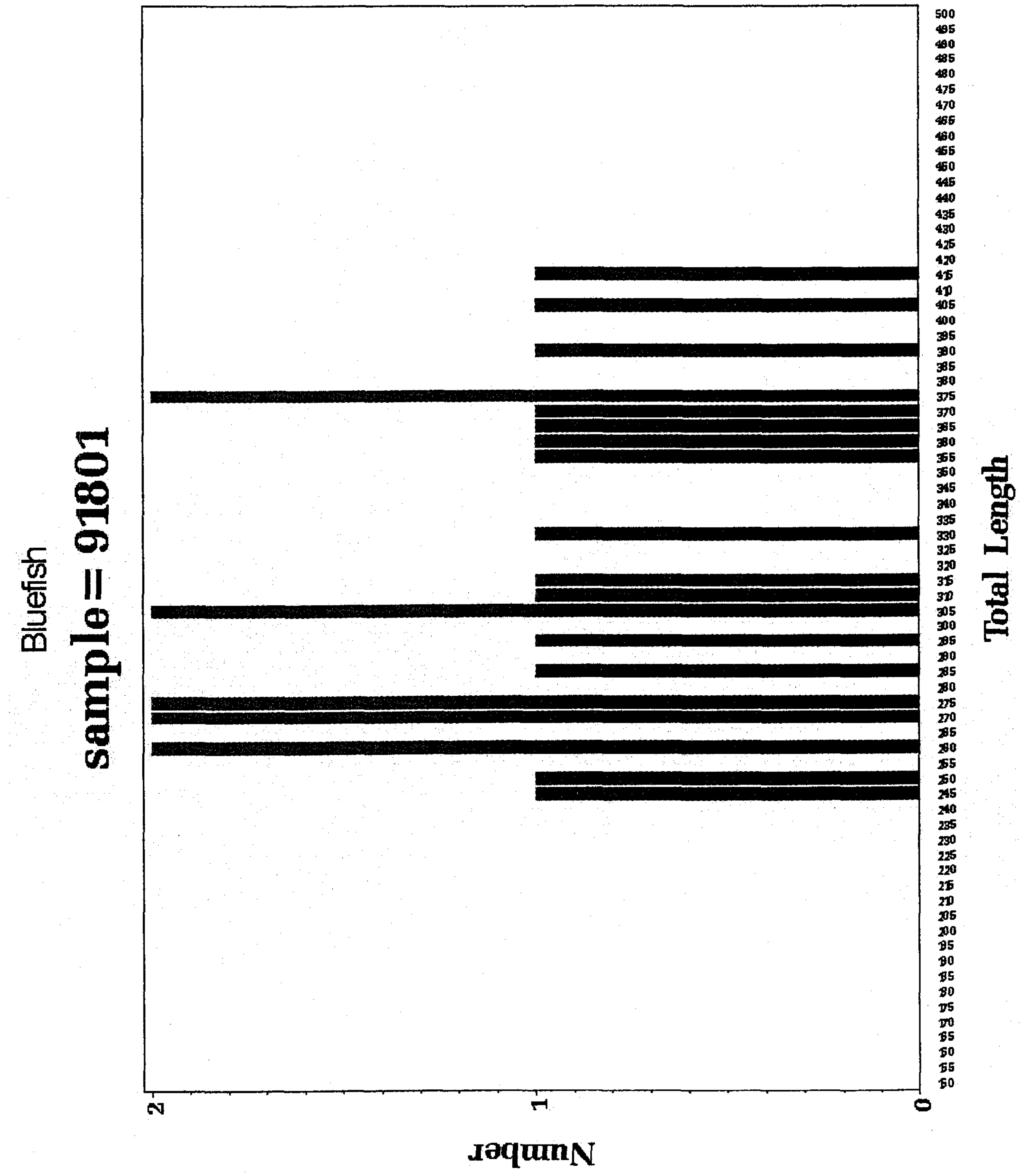
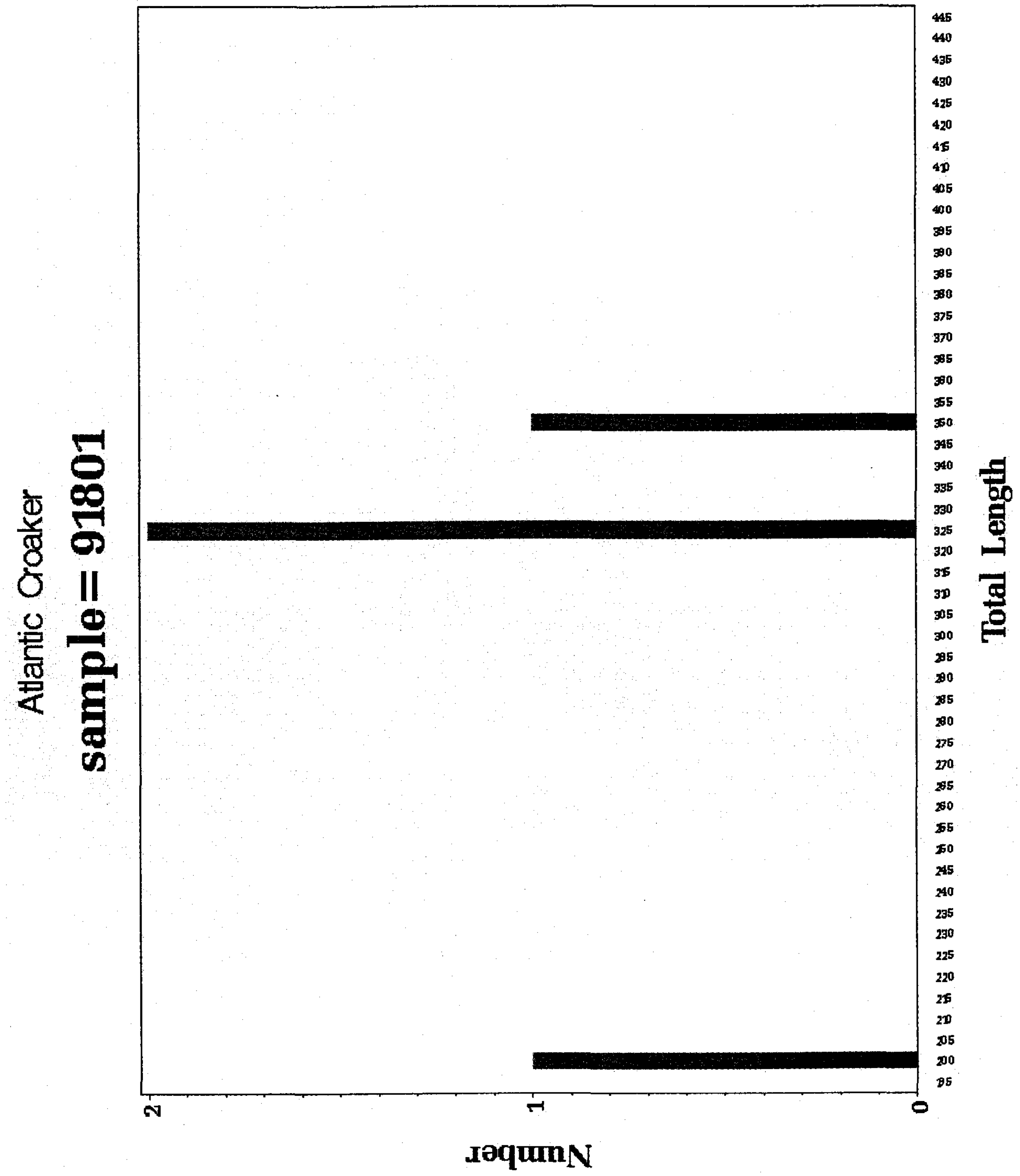
645
650



Bluefish

sample = 91801


Atlantic Croaker
sample=91801
Total Length
Number
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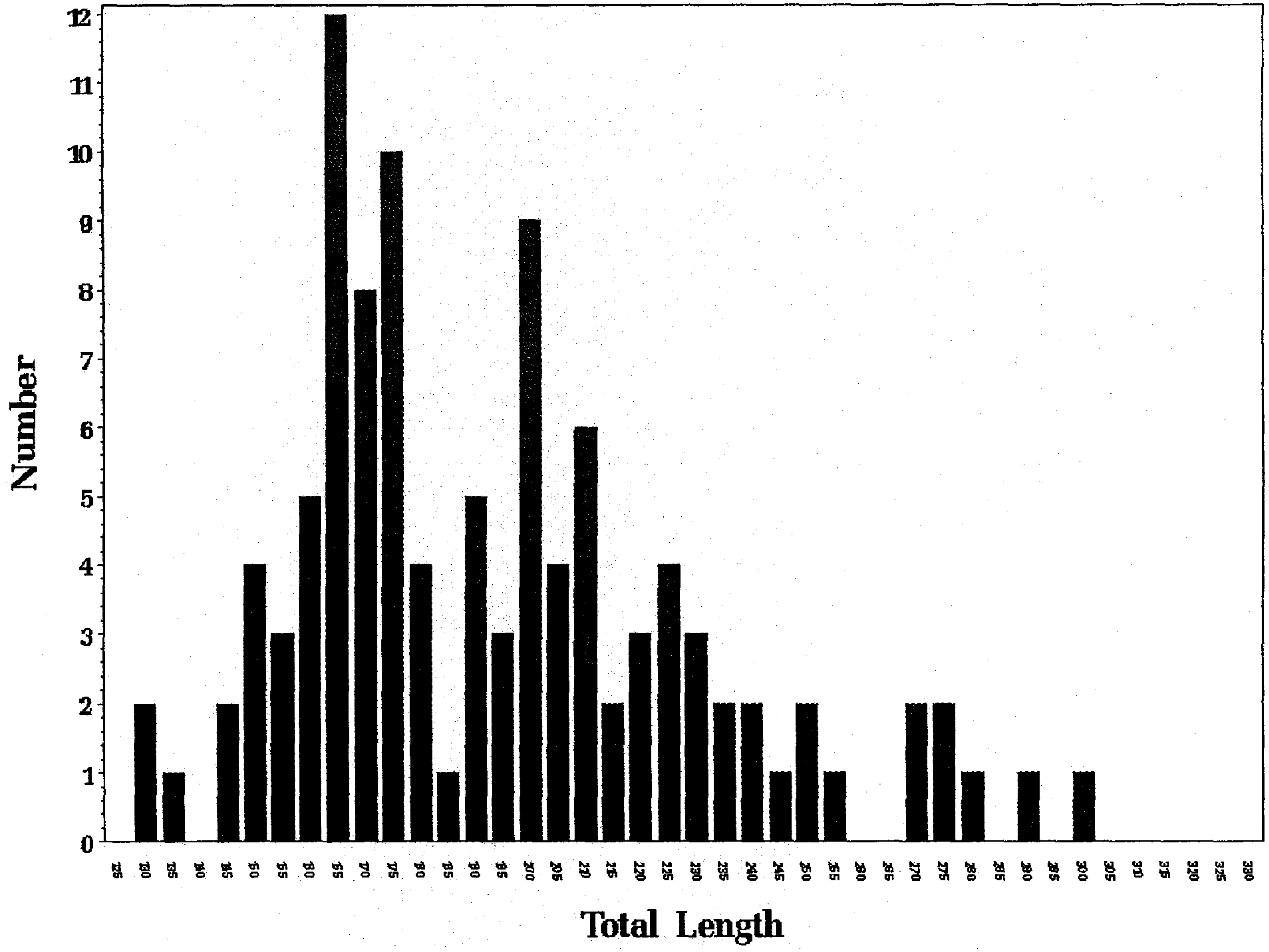
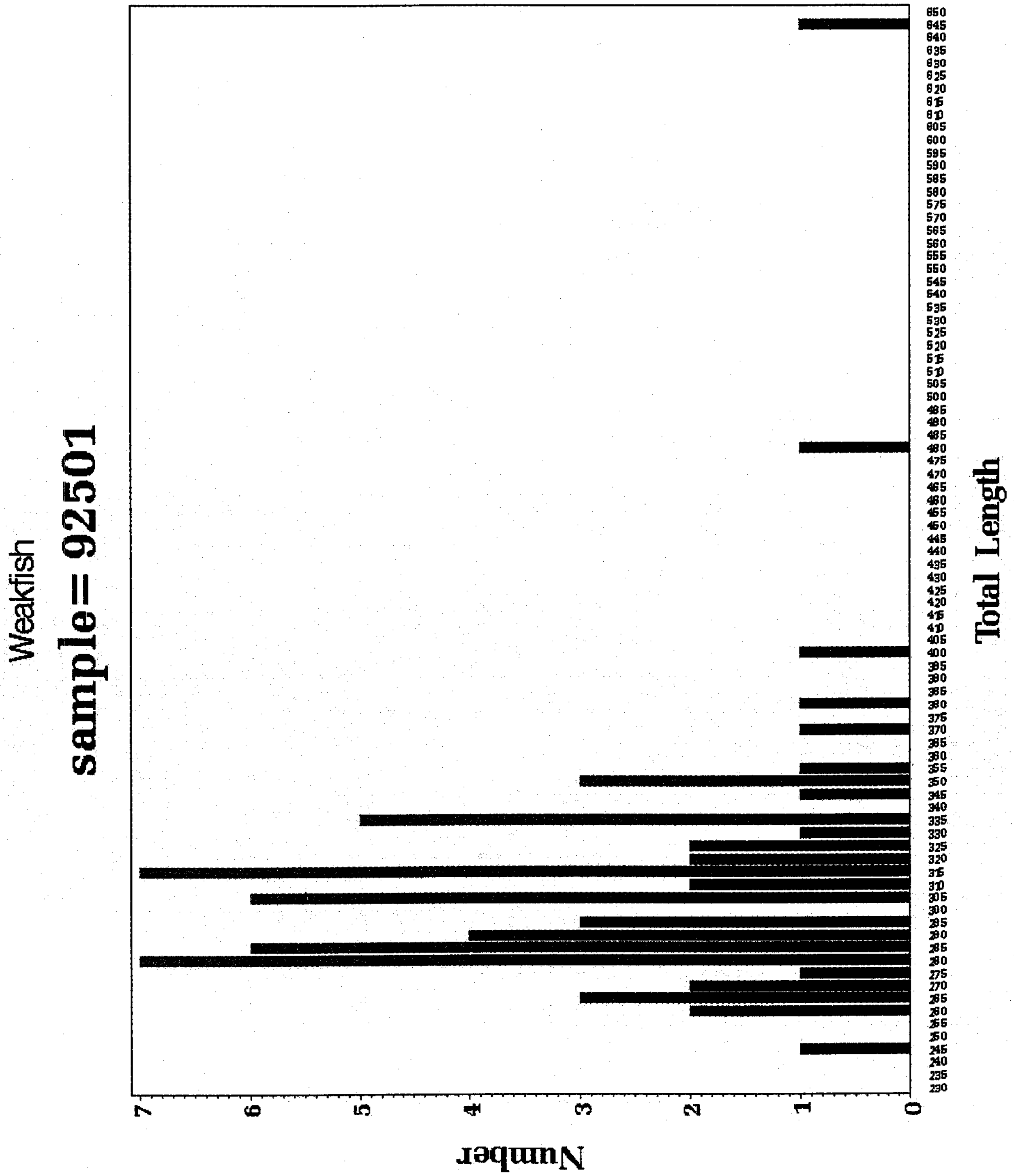
1
2
195
200
205
210
215
220
225
230
235
240
245
250
255
260
265
270
275
280
285
290
295
300
305
310
315
320
325
330
335
340
345
350
355
360
365
370
375
380
385
390
395
400
405
410
415
420
425
430
435
440
445

Spot

sample= 92501




Weakfish
sample= 92501
Number
0
1
2
3
4
5
6
7
Total Length
230
235
240
245
250
255
260
265
270
275
280
285
290
295
300
305
310
315
320
325
330
335
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365
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385
390
395
400
405
410
415
420
425
430
435
440
445
450
455
460
465
470
475
480
485
490
495
500
505
510
515
520
525
530
535
540
545
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560
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575
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600
605
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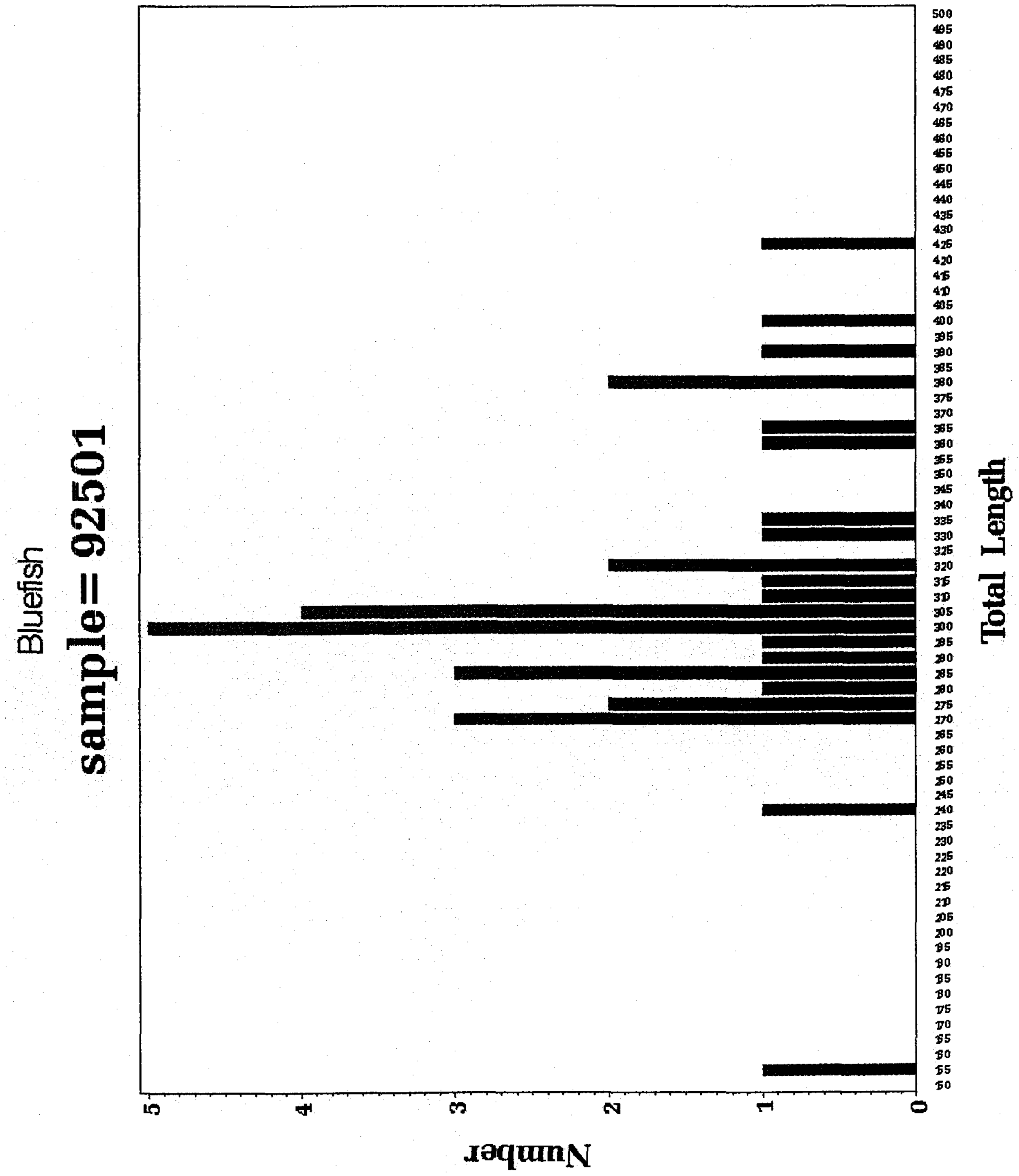
645
650


Bluefish
sample= 92501
Total Length
Number
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3
4
5
50
55
60
65
70
75
80
85
90
95
100
105
110
115
120
125
130
135
140
145
150
155
160
165
170
175
180
185
190
195
200
205
210
215
220
225
230
235
240
245
250
255
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300
305
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315
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385
390
395
400
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425
430
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440
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450
455
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465
470
475
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485
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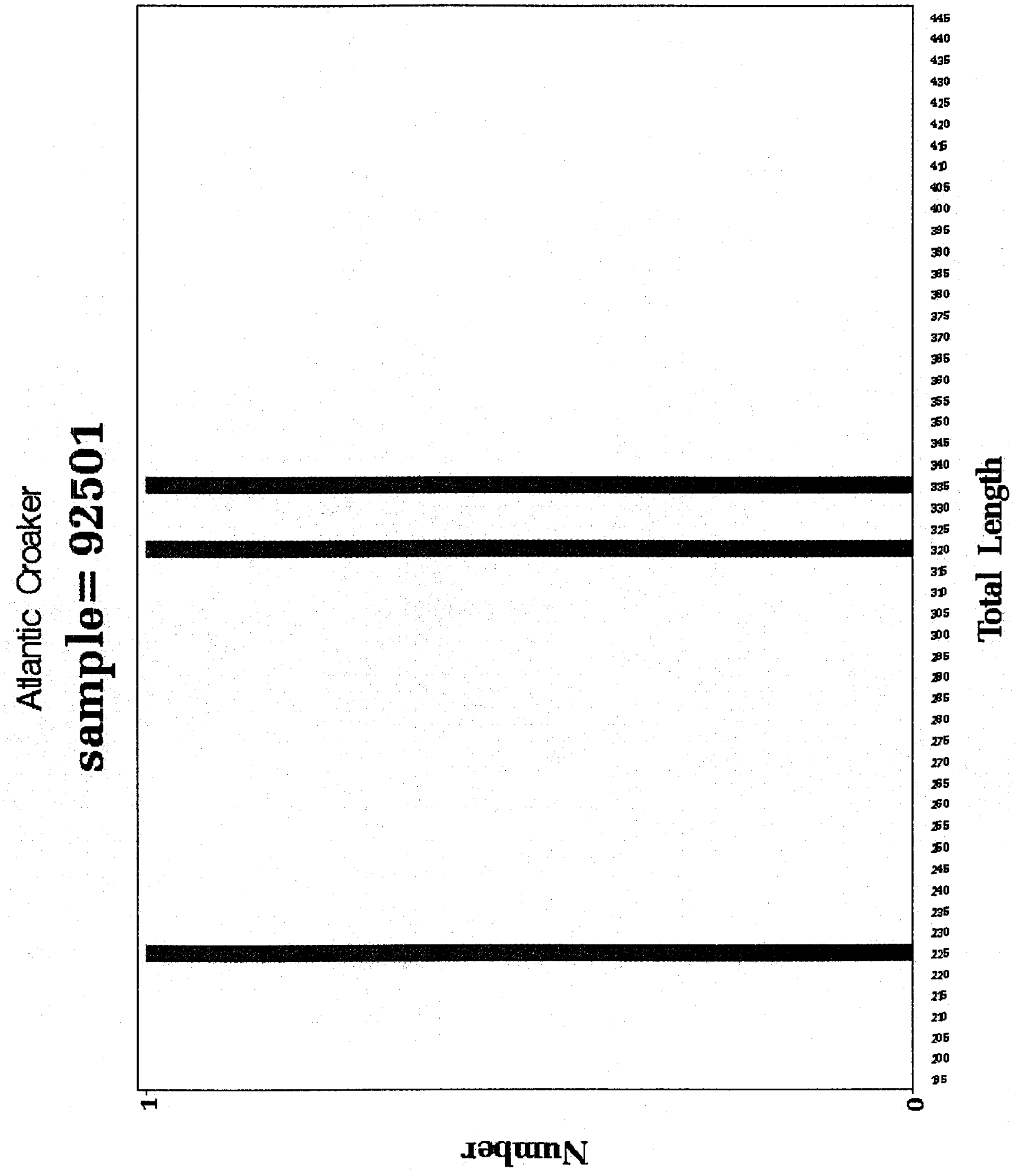
495
500


Atlantic Croaker
sample= 92501
Total Length
Number
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200
205
210
215
220
225
230
235
240
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250
255
260
265
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335
340
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375
380
385
390
395
400
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410
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420
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430
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440
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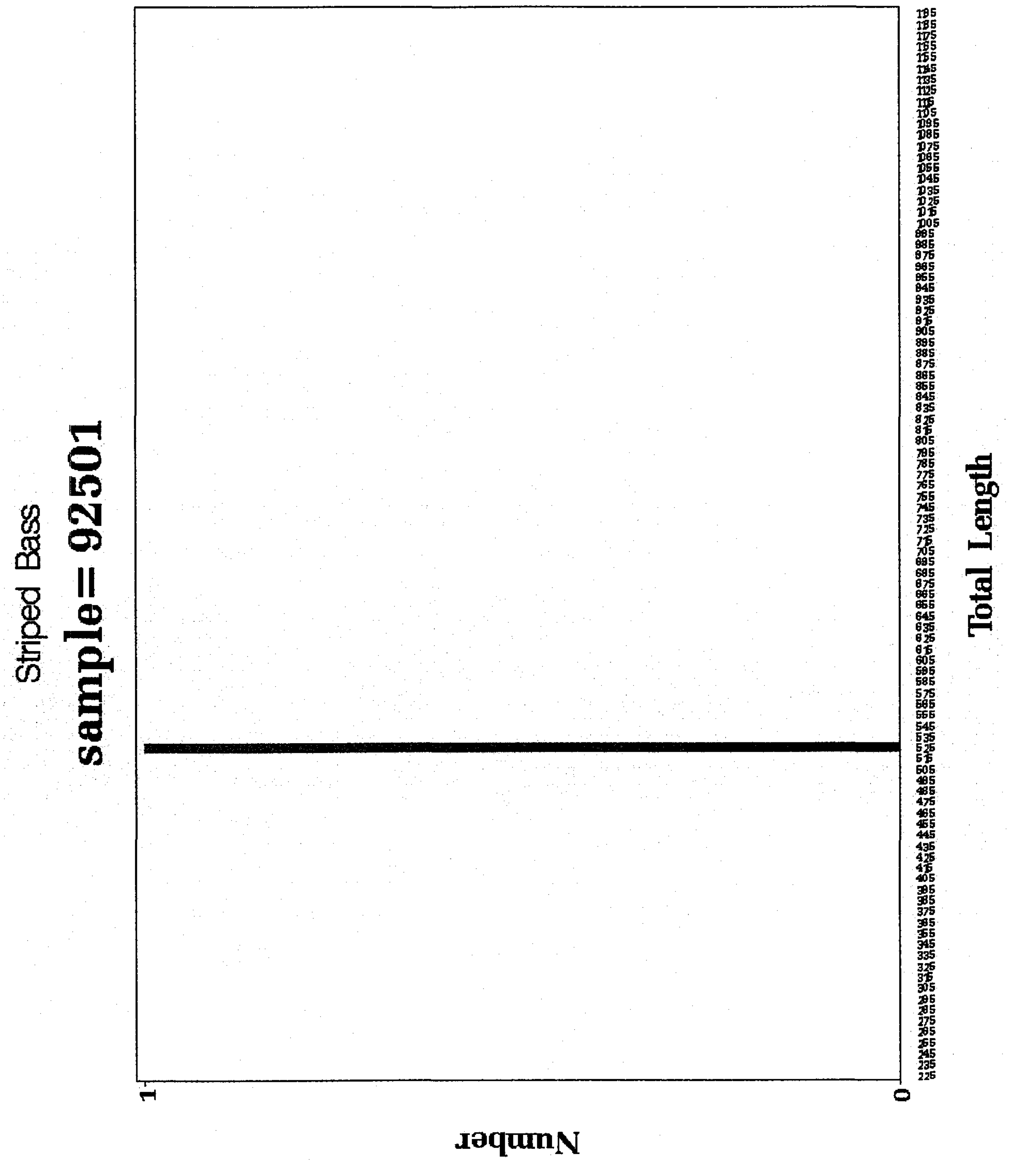
Striped Bass
sample= 92501
Number
Total Length
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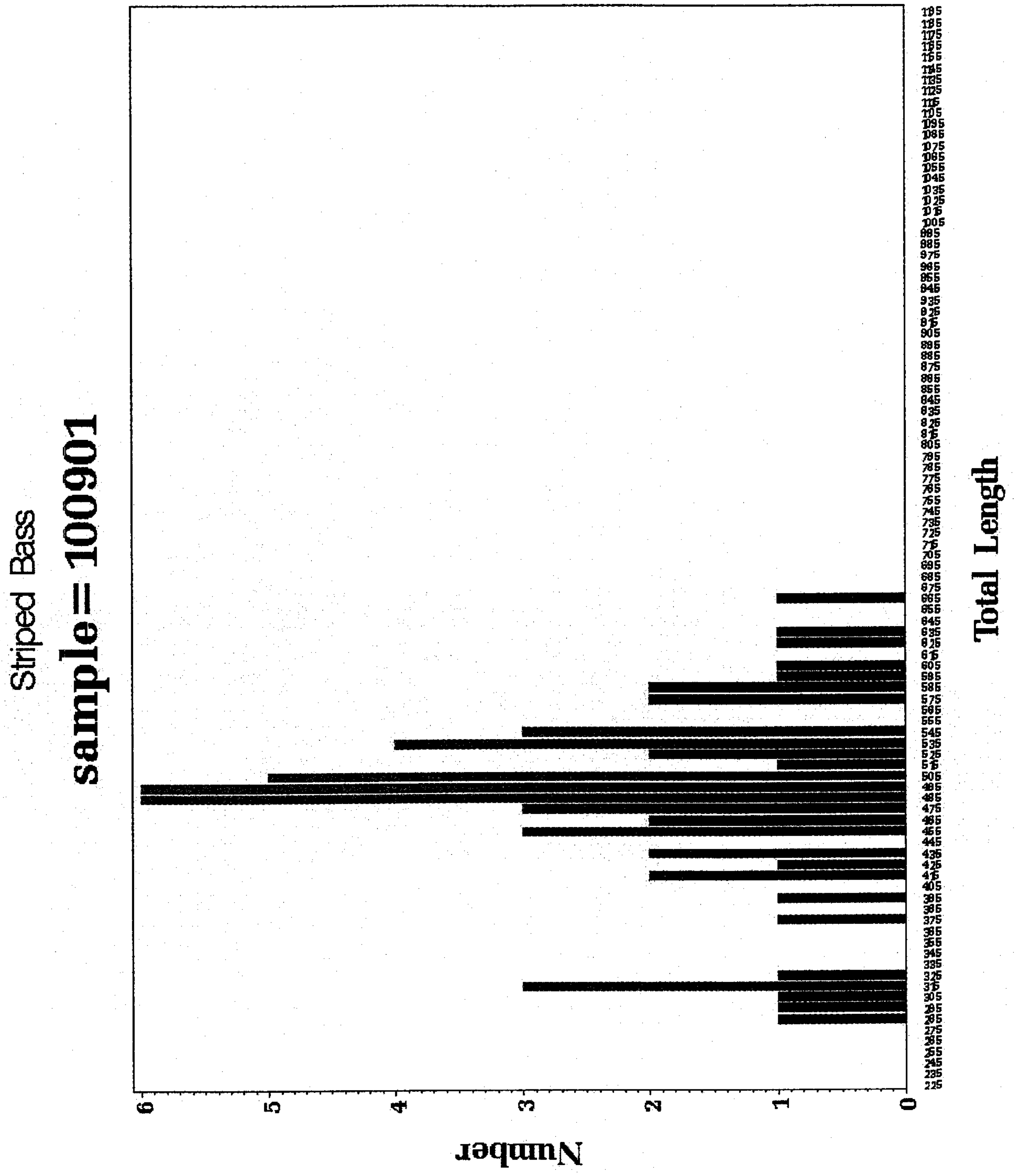
1


Striped Bass
sample= 100901
Number
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2
3
4
5
6
Total Length
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235
245
255
265
275
285
295
305
315
325
335
345
355
365
375
385
395
405
415
425
435
445
455
465
475
485
495
505
515
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605
615
625
635
645
655
665
675
685
695
705
715
725
735
745
755
765
775
785
795
805
815
825
835
845
855
865
875
885
895
905
915
925
935
945
955
965
975
985
995
1005
1015
1025
1035
1045
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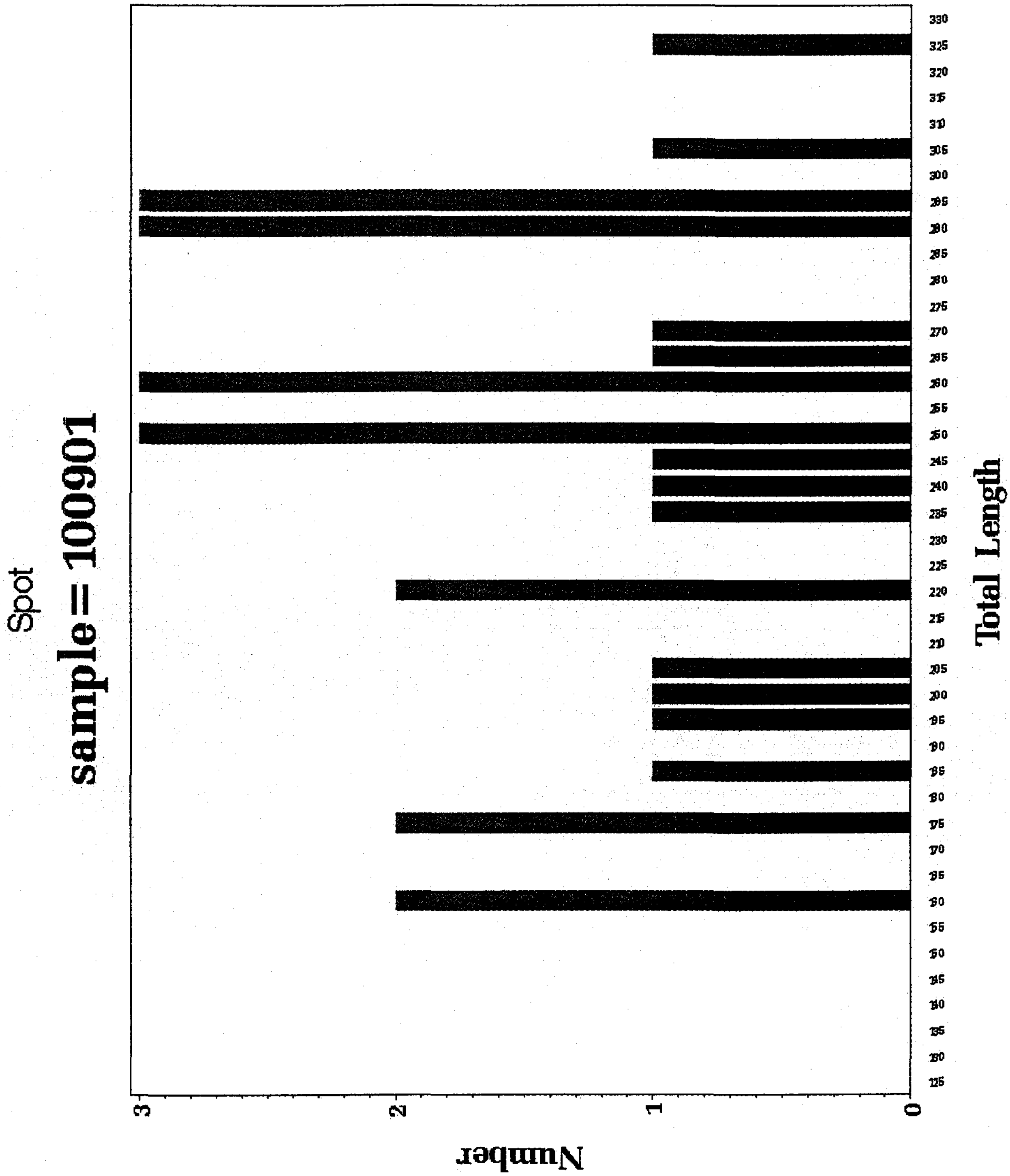
1155
1165
1175
1185
1195


Spot
sample=100901
Number
0
1
2
3
Total Length
125
130
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140
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150
155
160
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170
175
180
185
190
195
200
205
210
215
220
225
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255
260
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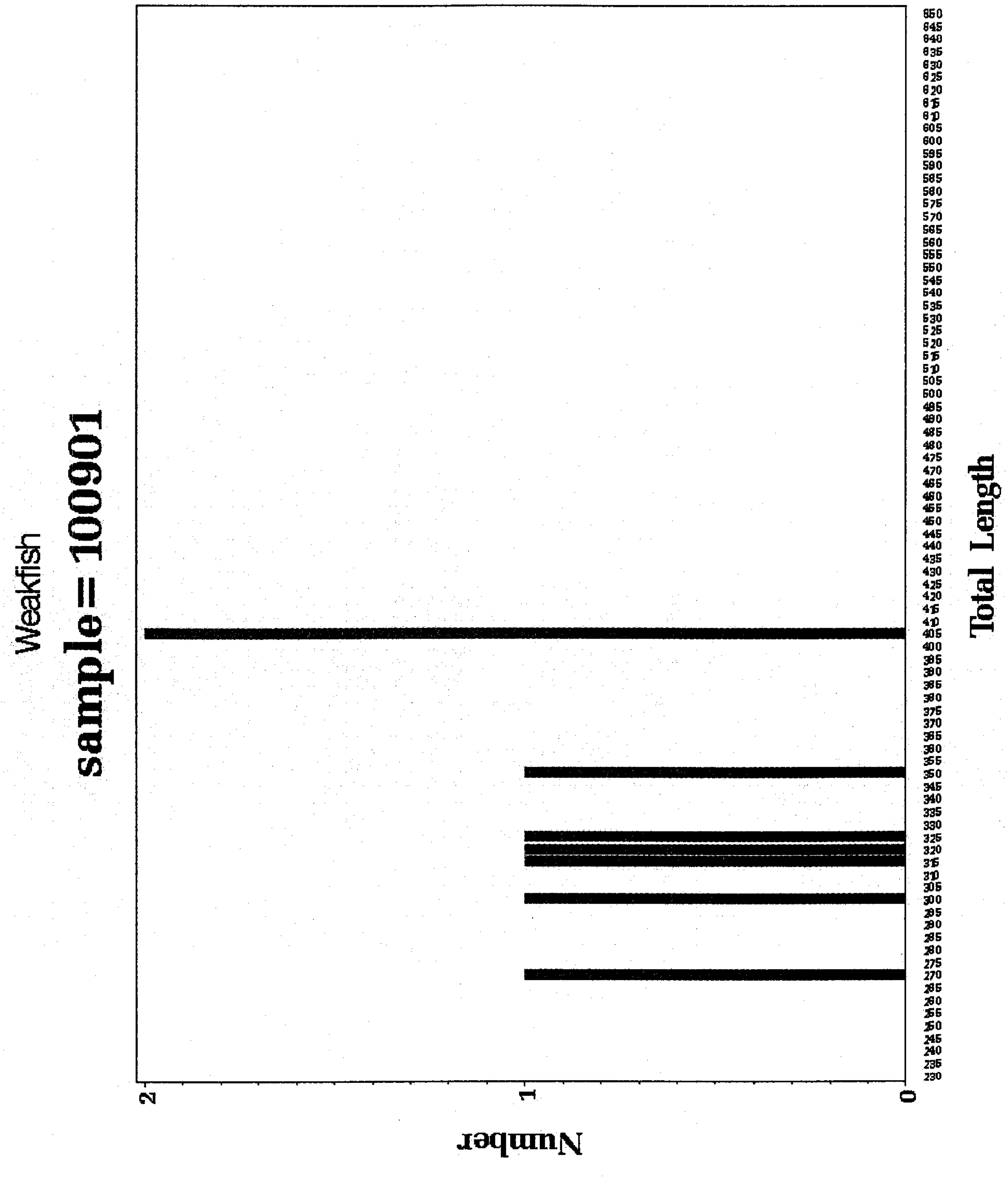
Weakfish
sample=100901
Number
0
1
2
Total Length
230
235
240
245
250
255
260
265
270
275
280
285
290
295
300
305
310
315
320
325
330
335
340
345
350
355
360
365
370
375
380
385
390
395
400
405
410
415
420
425
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450
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460
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475
480
485
490
495
500
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510
515
520
525
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535
540
545
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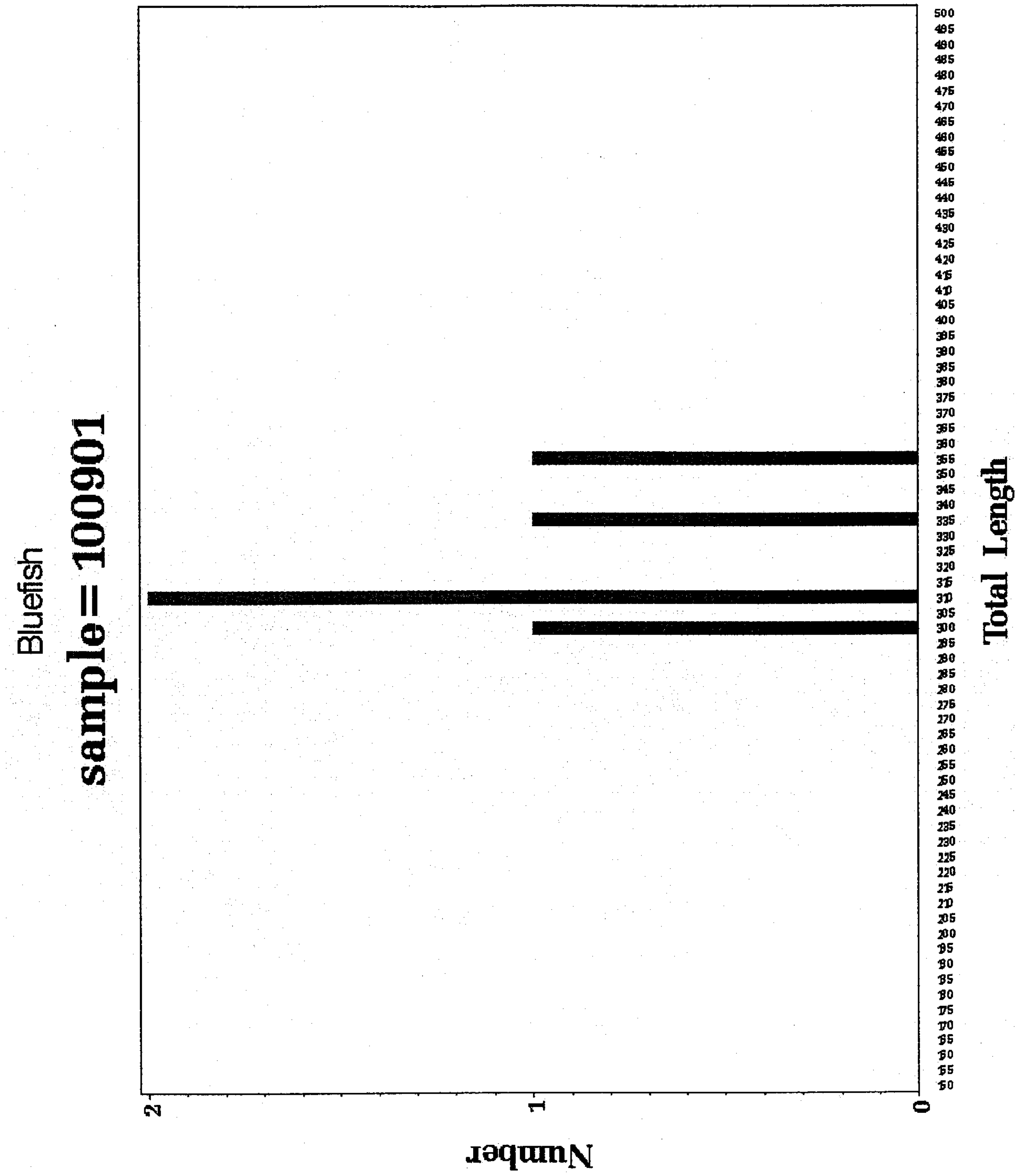
Bluefish
sample= 100901
Number
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1
2
Total Length
50
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80
85
90
95
100
105
110
115
120
125
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135
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145
150
155
160
165
170
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180
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385
390
395
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425
430
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445
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465
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485
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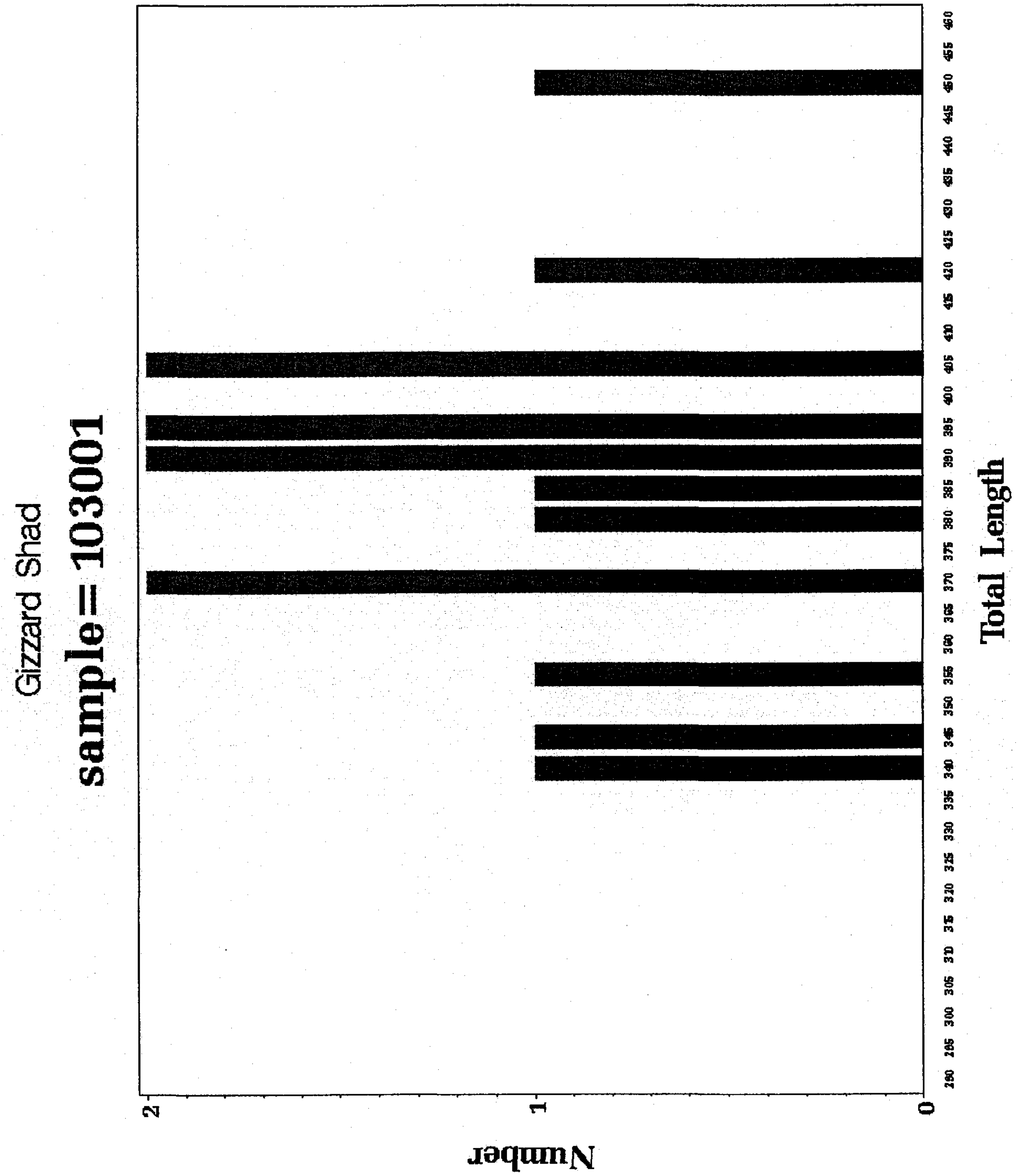
495
500


Gizzard Shad
sample= 103001
Number
0
1
2
Total Length
290
295
300
305
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315
320
325
330
335
340
345
350
355
360
365
370
375
380
385
390
395
400
405
410
415
420
425
430
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445
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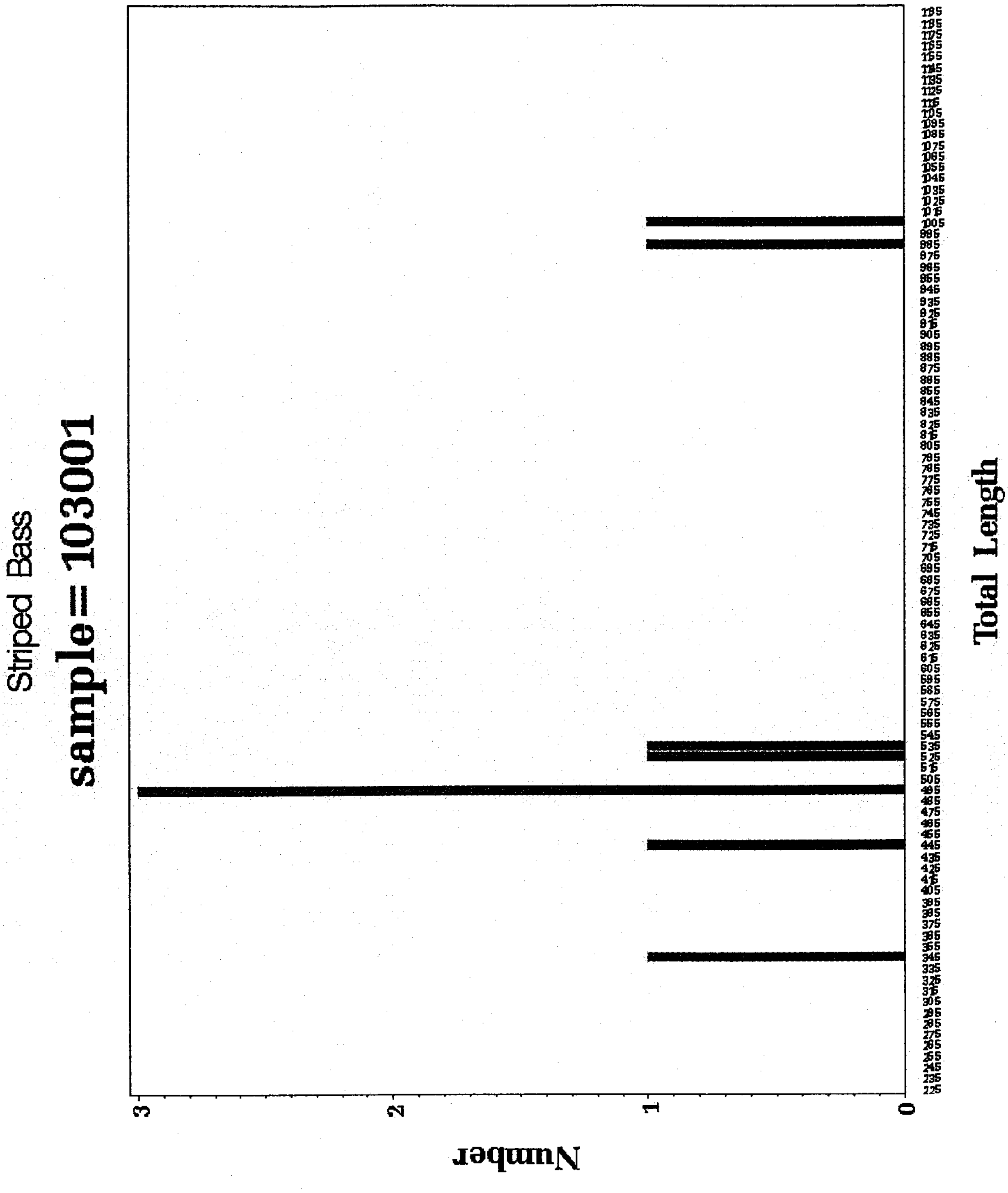
460


Striped Bass
sample=103001
Number
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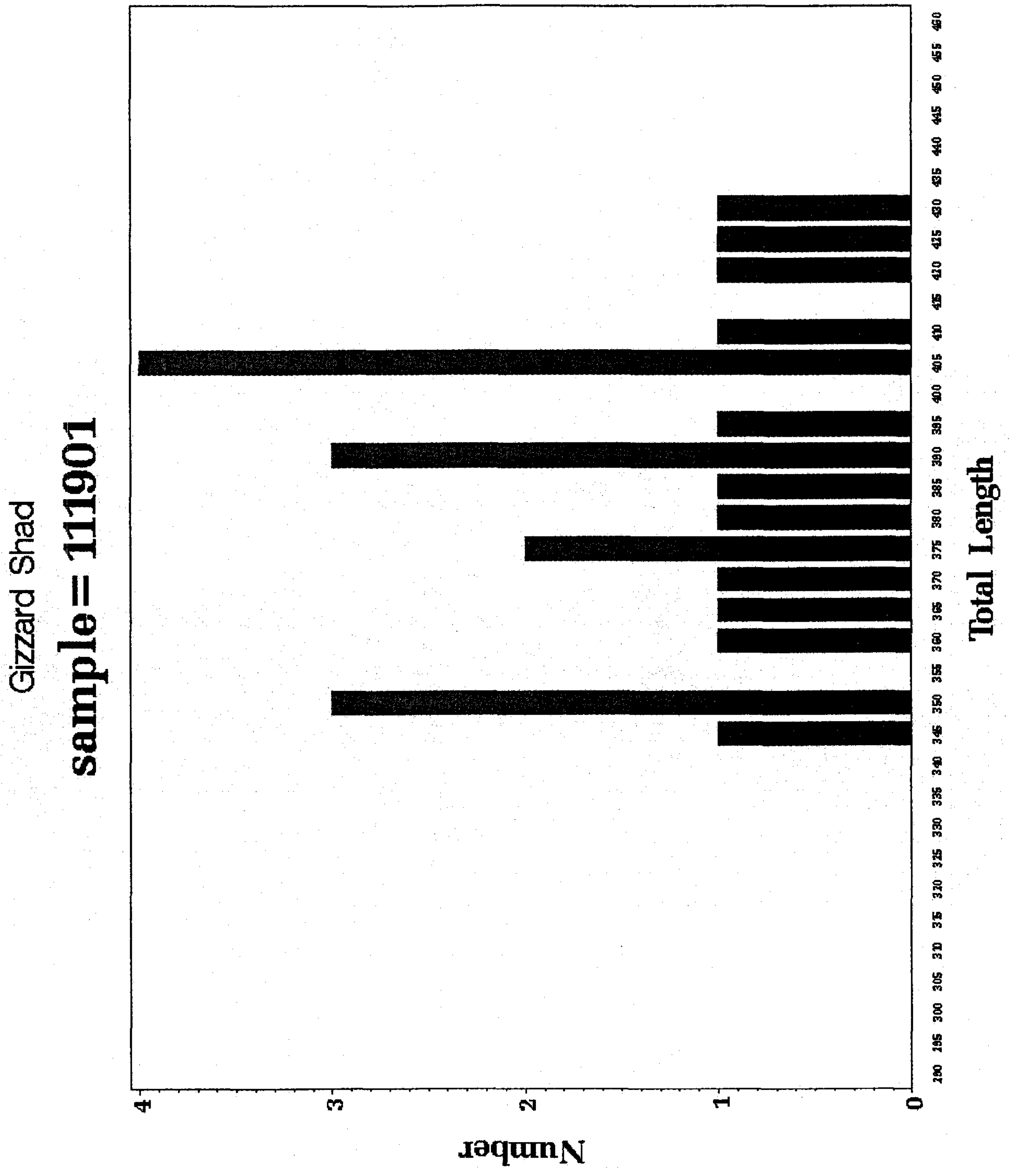
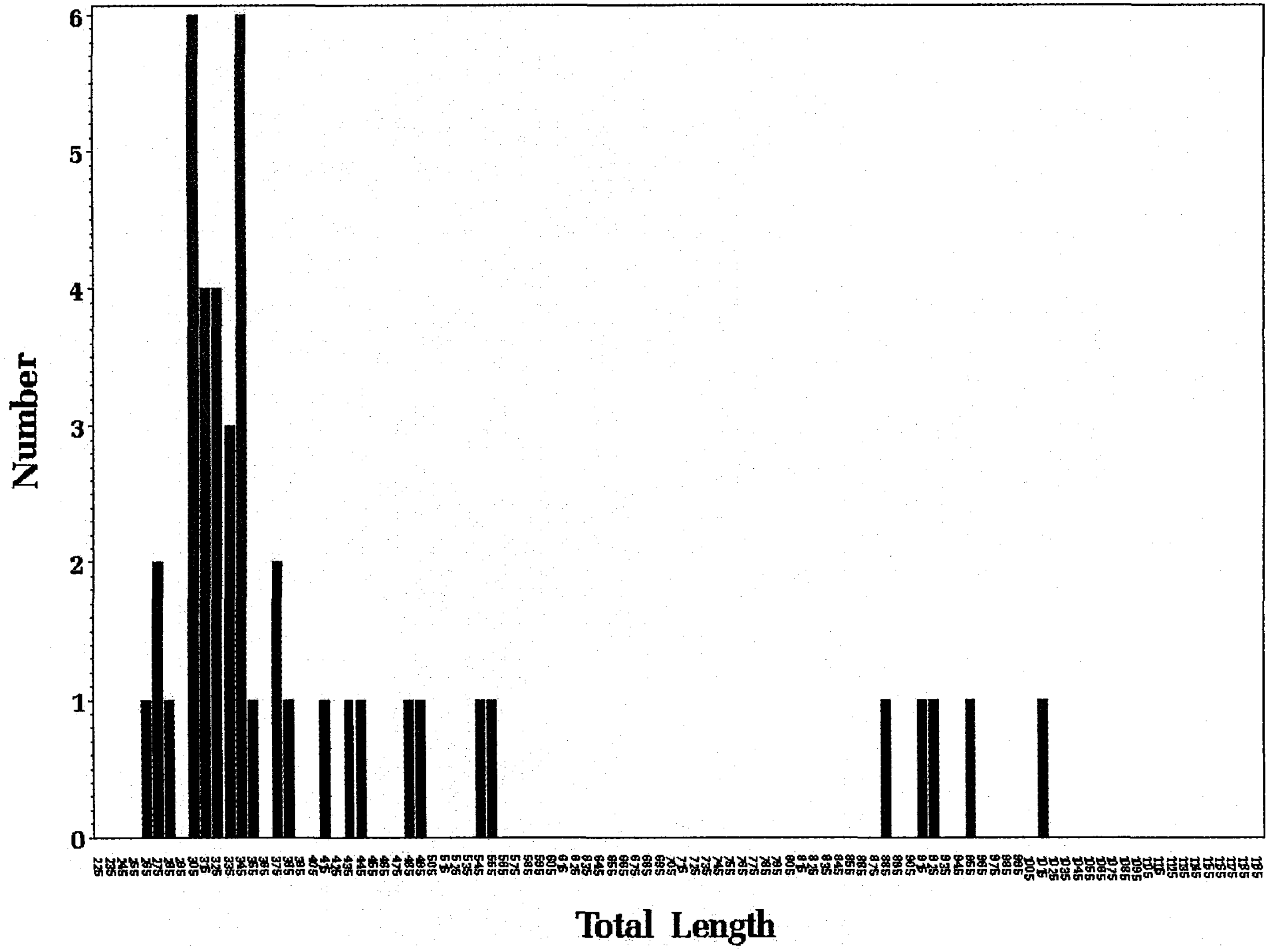
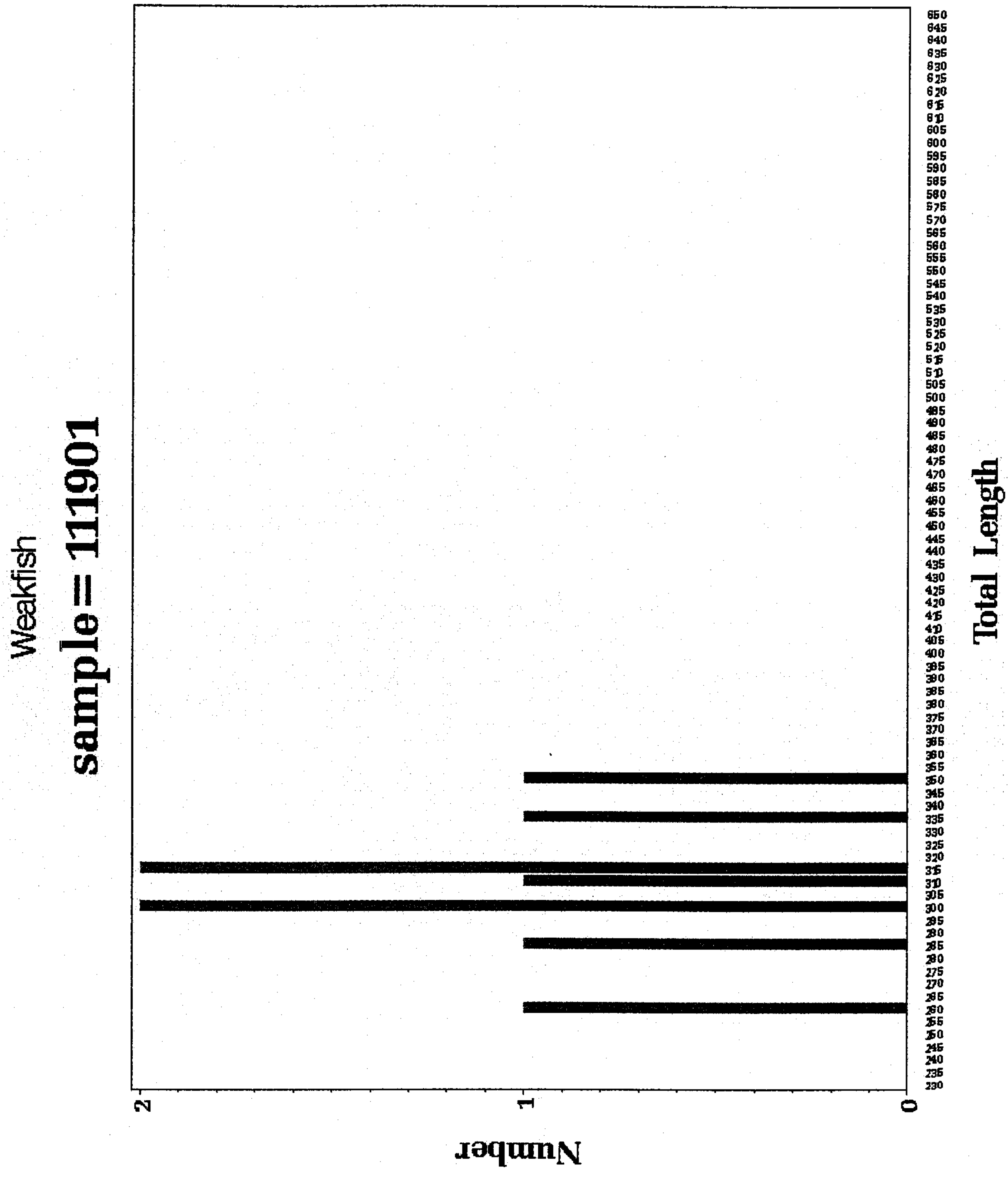
1
2
3
Total Length


Gizzard Shad
sample= 111901
Number
0
1
2
3
4
Total Length
290
295
300
305
310
315
320
325
330
335
340
345
350
355
360
365
370
375
380
385
390
395
400
405
410
415
420
425
430
435
440
445
450
455
460

Striped Bass

sample= 111901




Weakfish
sample= 111901
Number
0
1
2
Total Length
230
235
240
245
250
255
260
265
270
275
280
285
290
295
300
305
310
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330
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400
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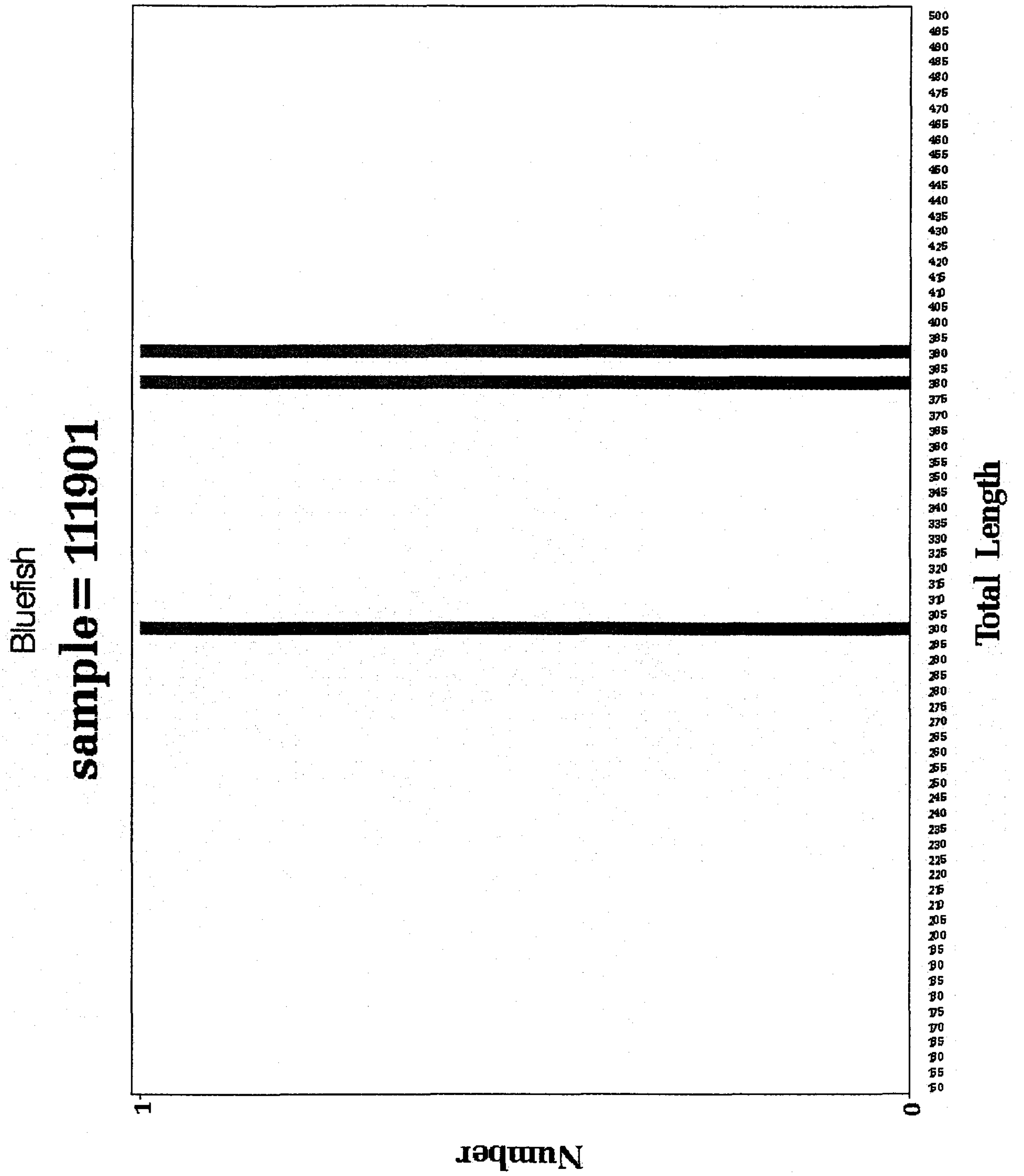
Bluefish
sample=111901
Total Length
Number
0
1
500
495
490
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480
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465
460
455
450
445
440
435
430
425
420
415
410
405
400
395
390
385
380
375
370
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360
355
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345
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295
290
285
280
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265
260
255
250
245
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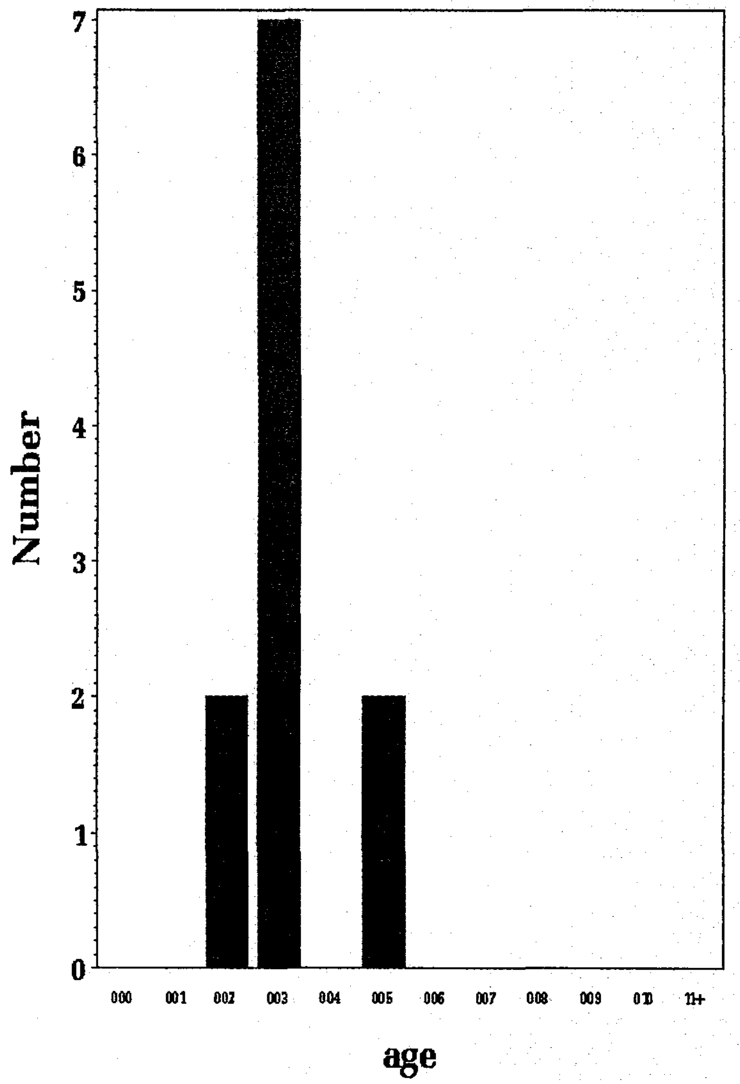
160
155
150
145
140
135
130
125
120
115
110
105
100
95
90
85
80
75
70
65
60

Appendix 7. This appendix contains the age distributions per sample for striped bass, bluefish, and weakfish as determined by length age equations. Distributions are listed in sample order followed by abundance.

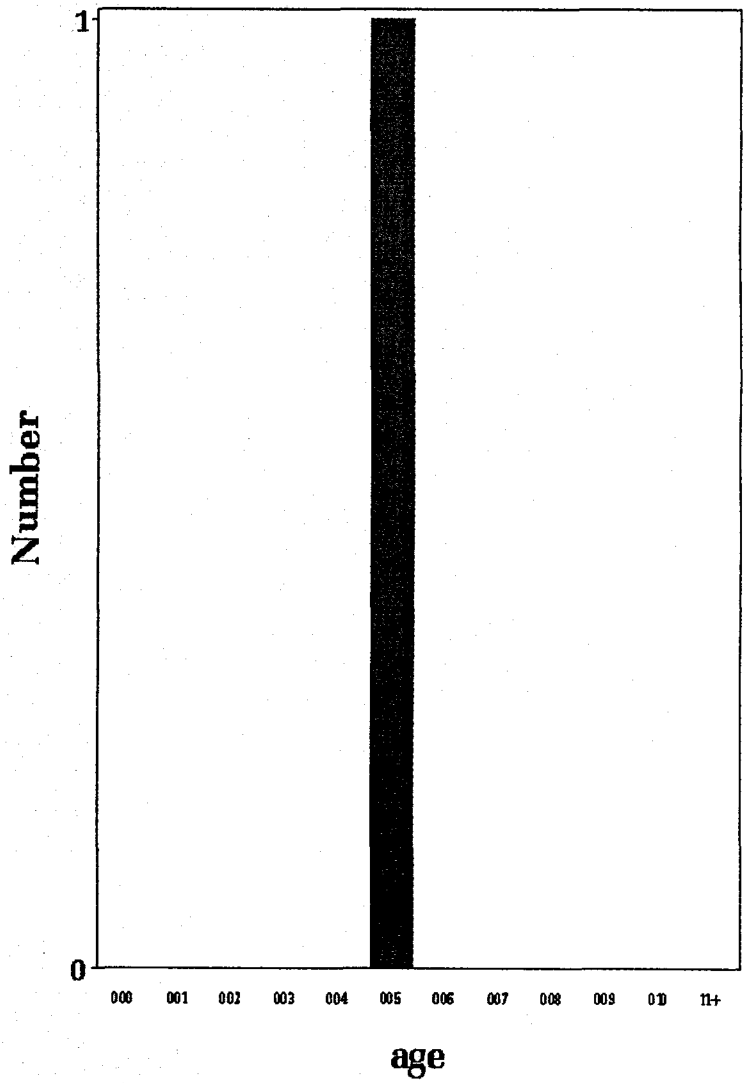
Striped bass Age Distribution

sample= 41201



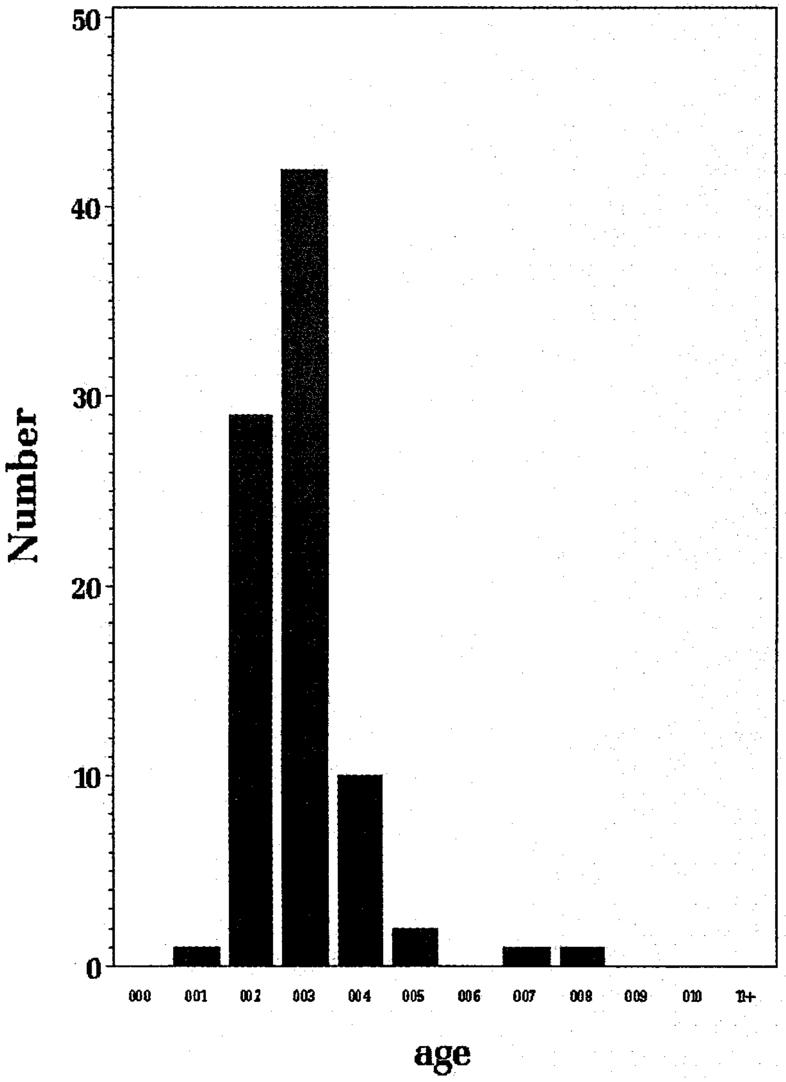
Striped bass Age Distribution

sample= 42501



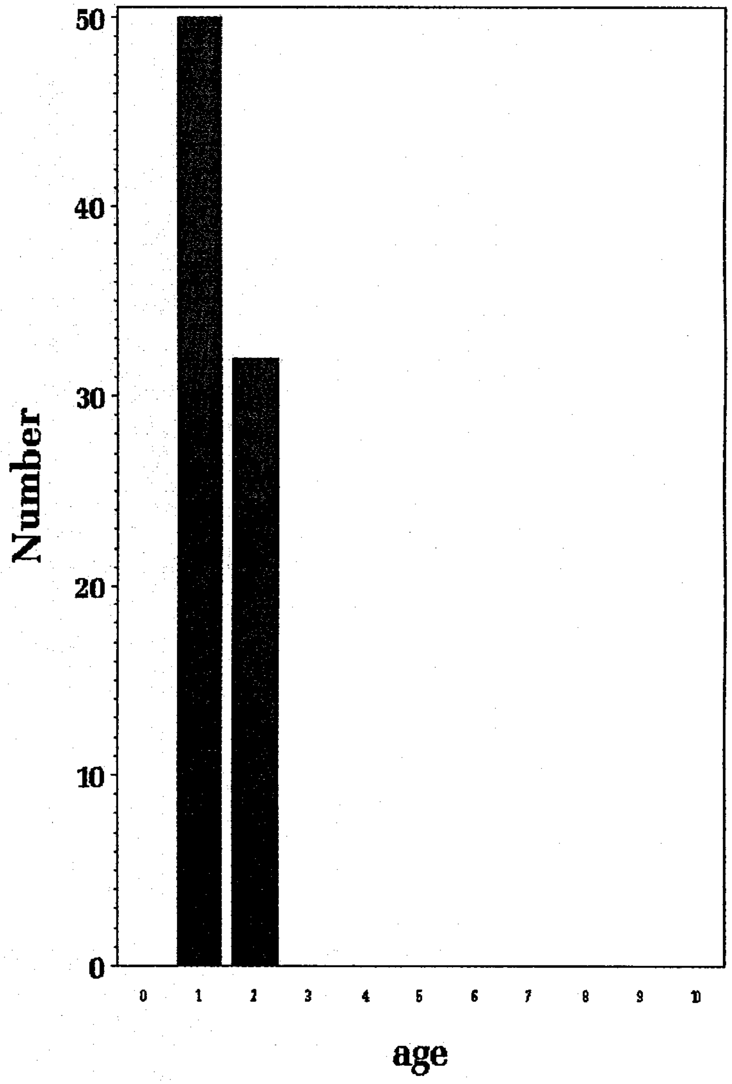
Striped bass Age Distribution

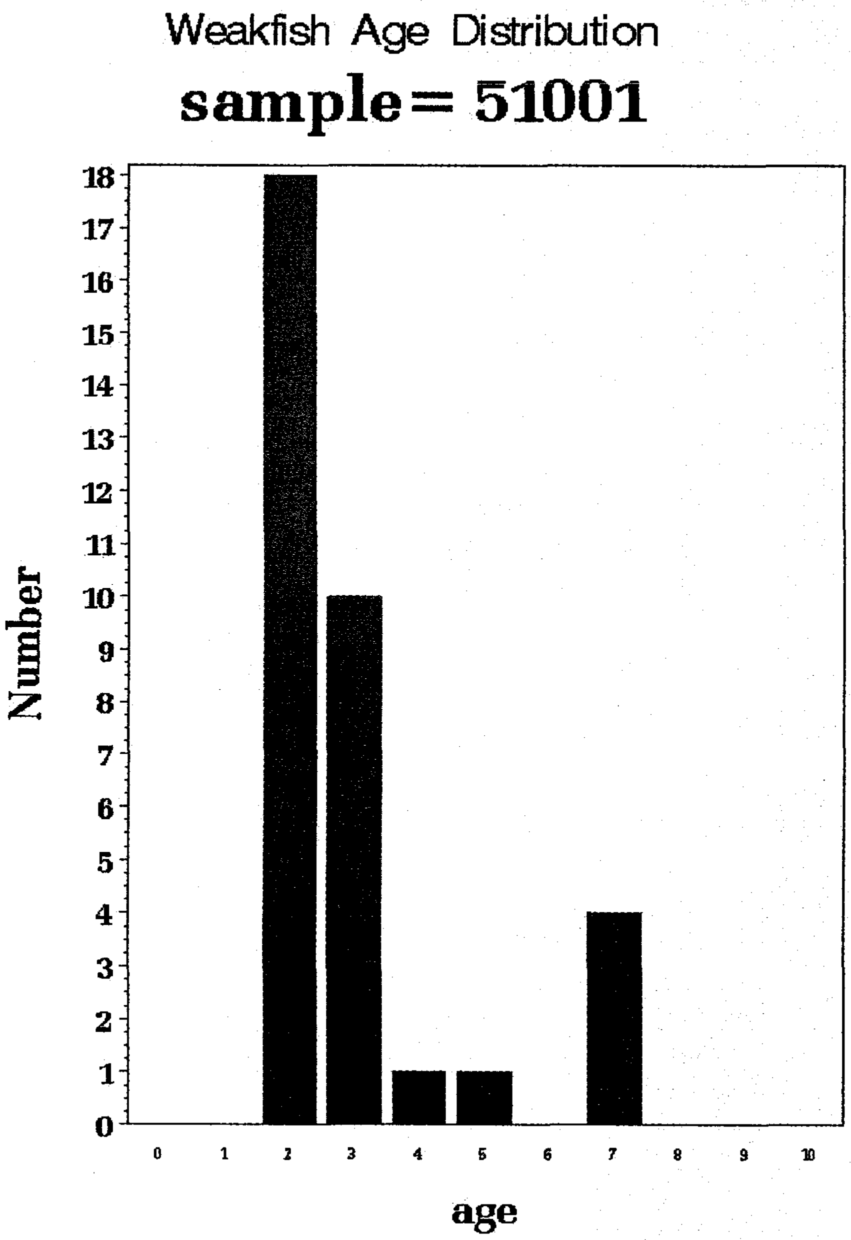
sample= 51001

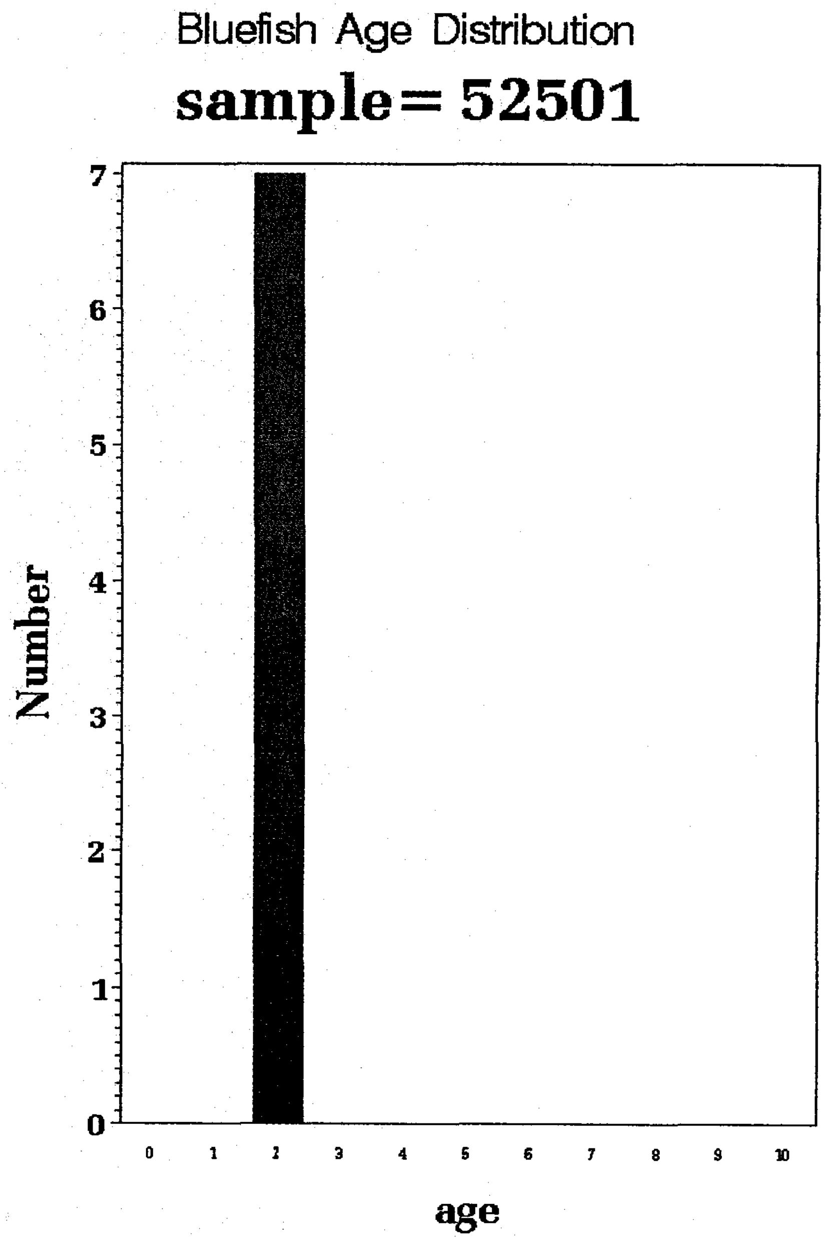


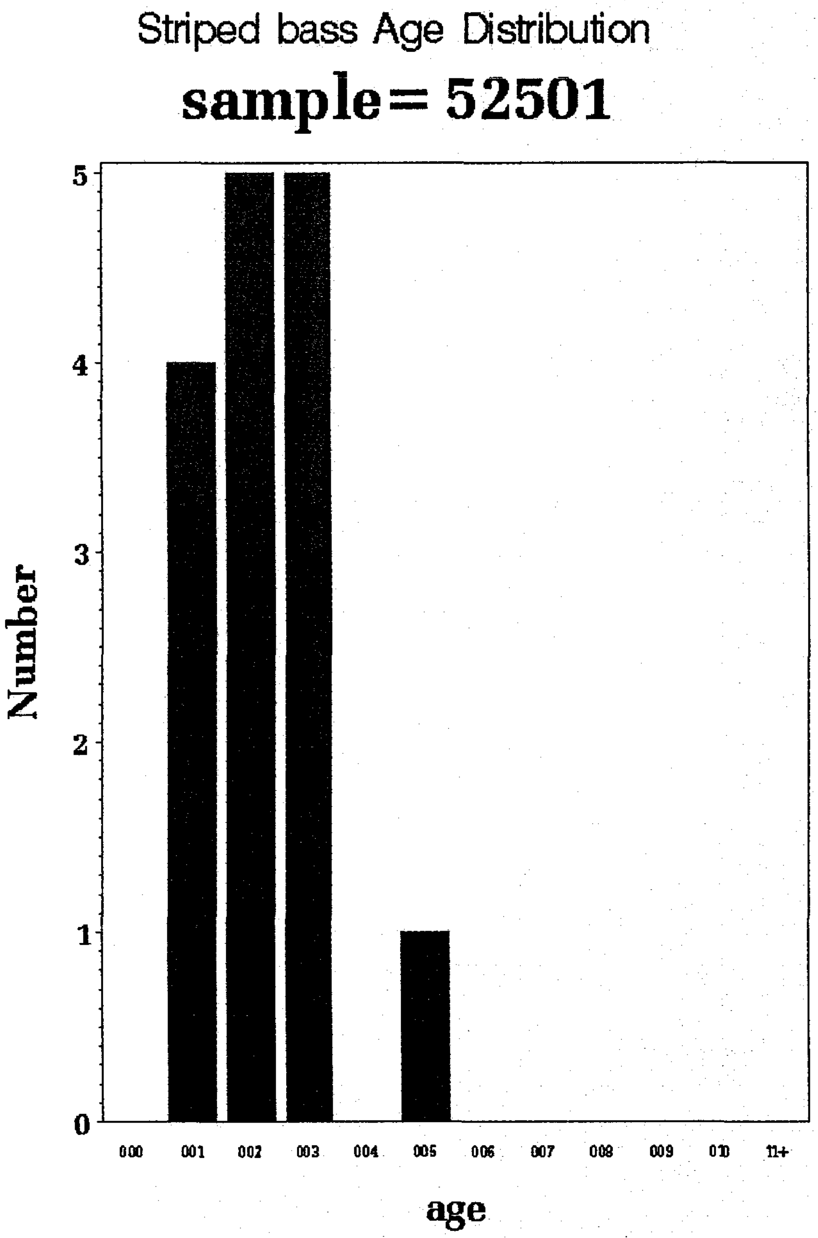
Bluefish Age Distribution

sample= 51001



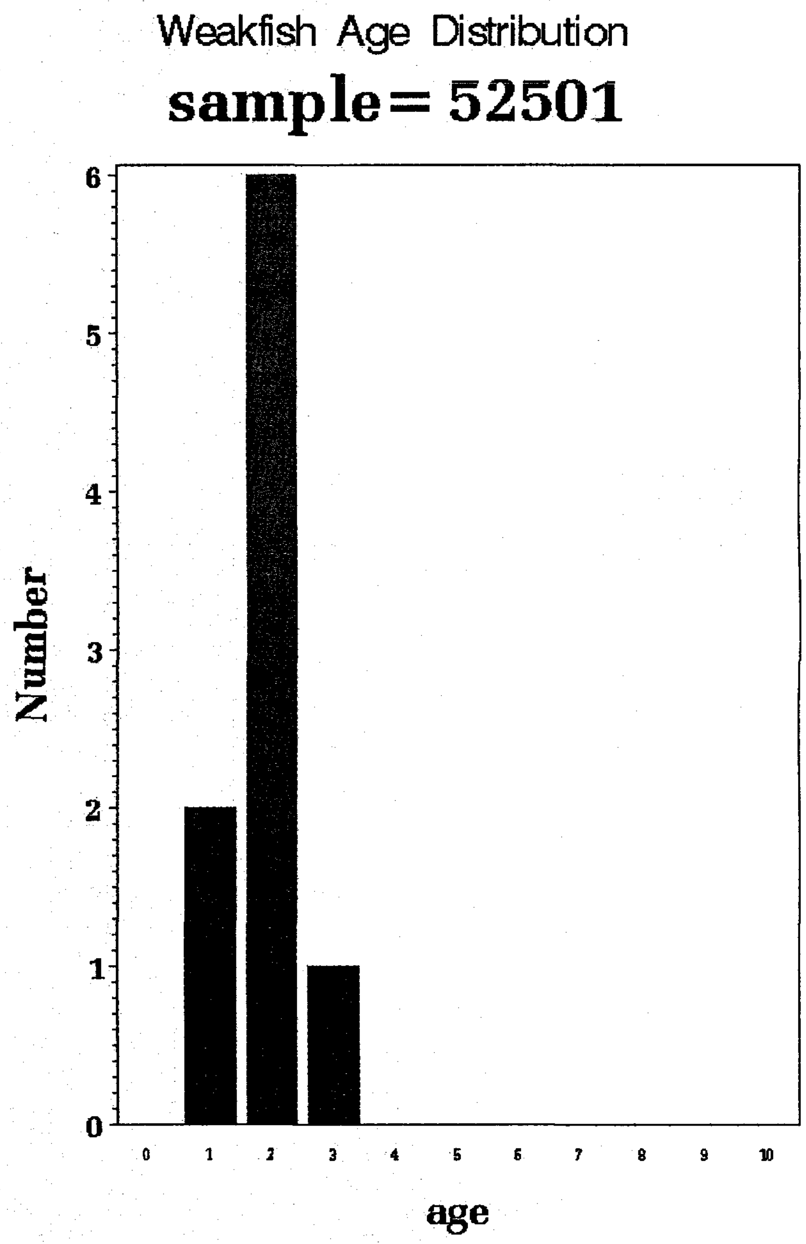

Weakfish Age Distribution
sample= 51001
Number
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
age
0
1
2
3
4
5
6
7
8
9
10


Bluefish Age Distribution
sample= 52501
Number
0
1
2
3
4
5
6
7
age
0
1
2
3
4
5
6
7
8
9
10



Striped bass Age Distribution

sample= 52501

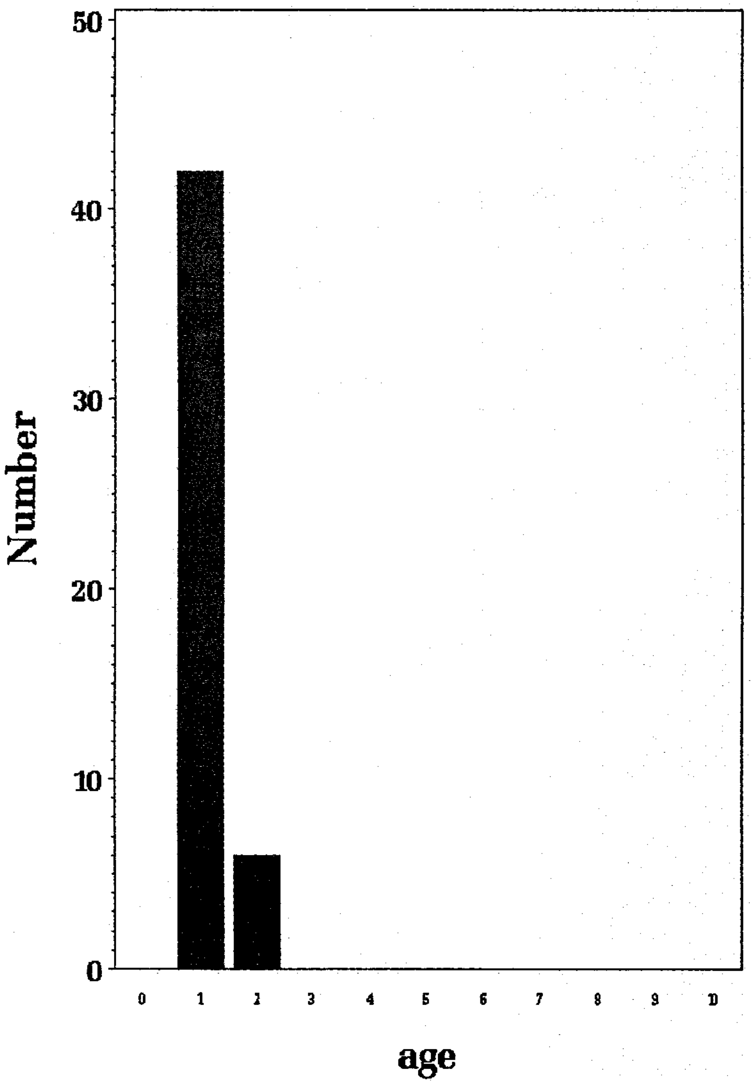


Weakfish Age Distribution

sample= 52501

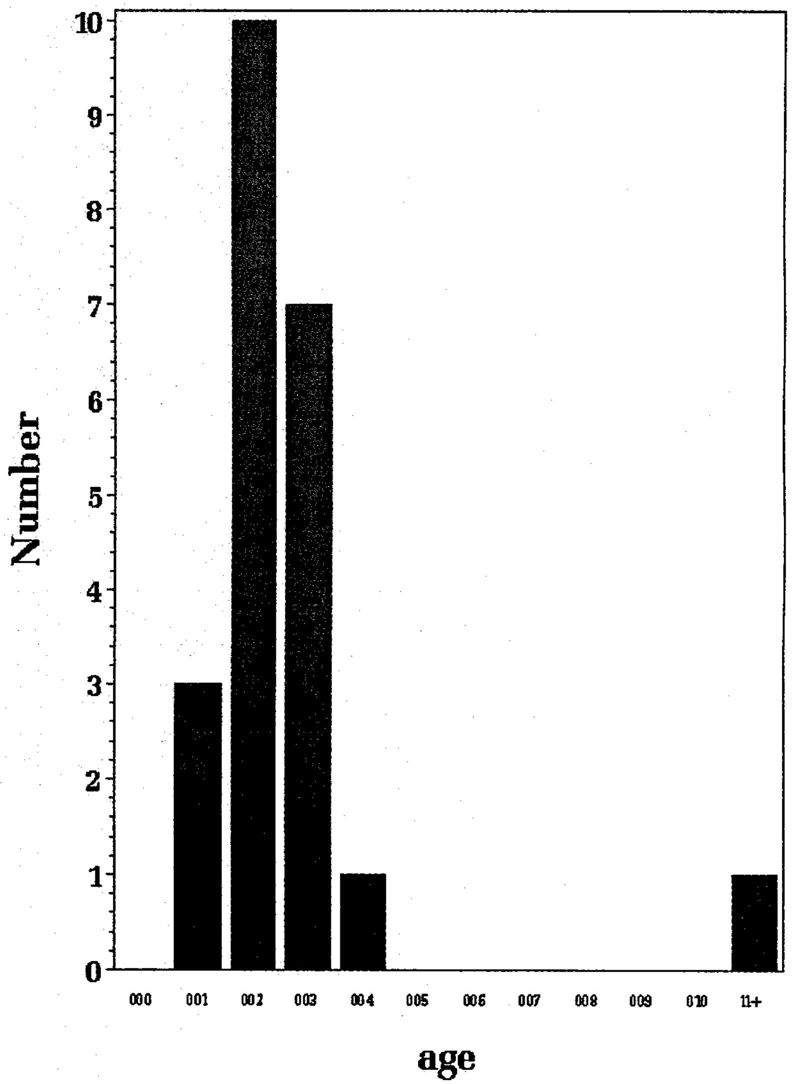
Bluefish Age Distribution

sample= 61201

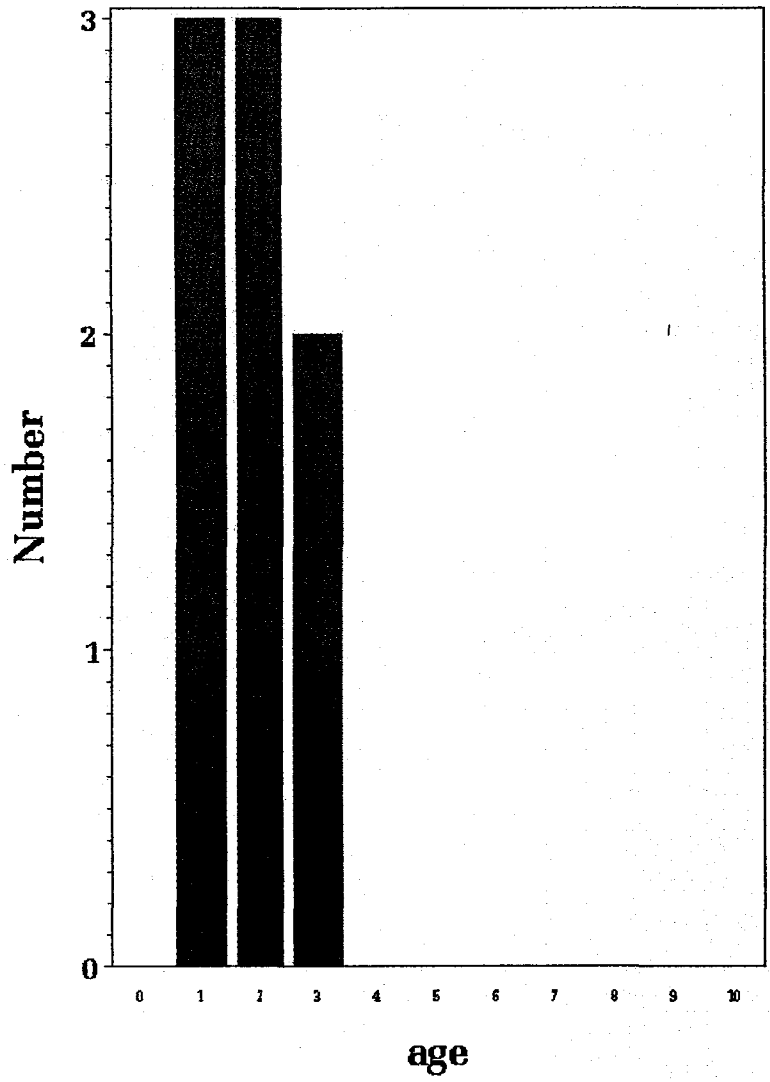


Striped bass Age Distribution

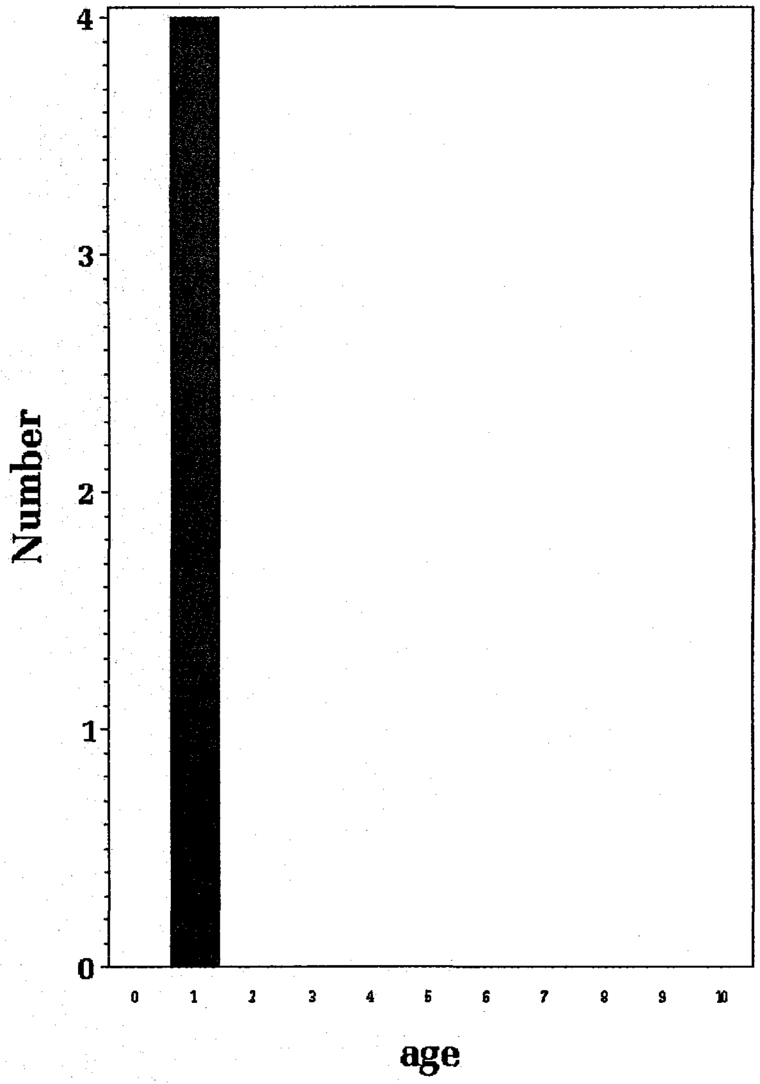
sample= 61201

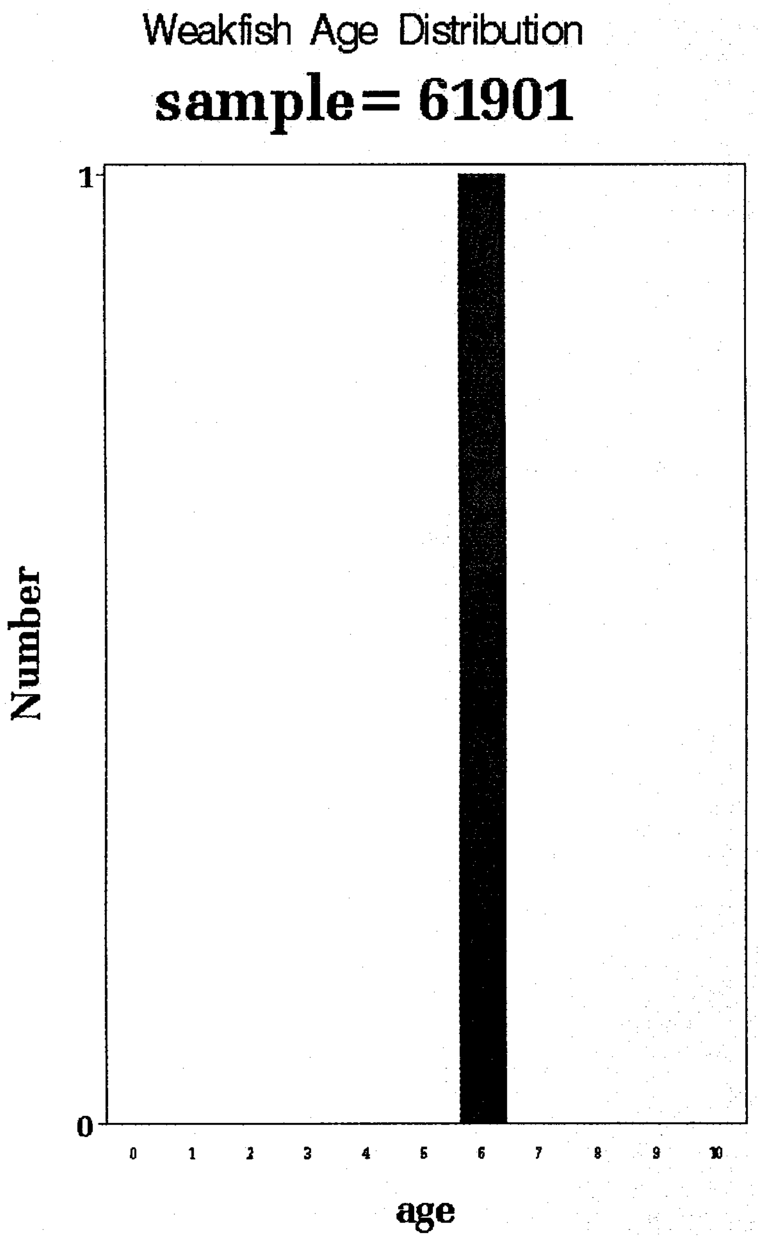


Weakfish Age Distribution
sample= 61201



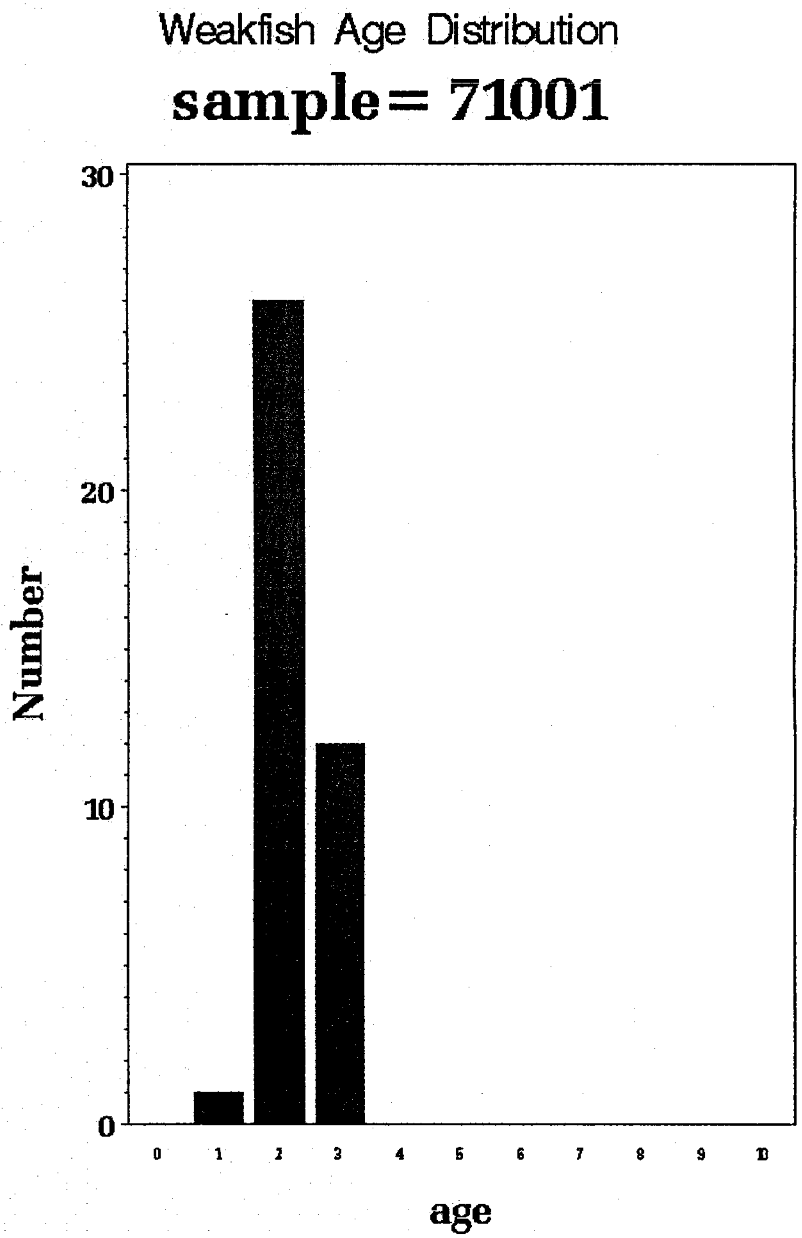
Bluefish Age Distribution
sample= 61901





Weakfish Age Distribution

sample= 61901

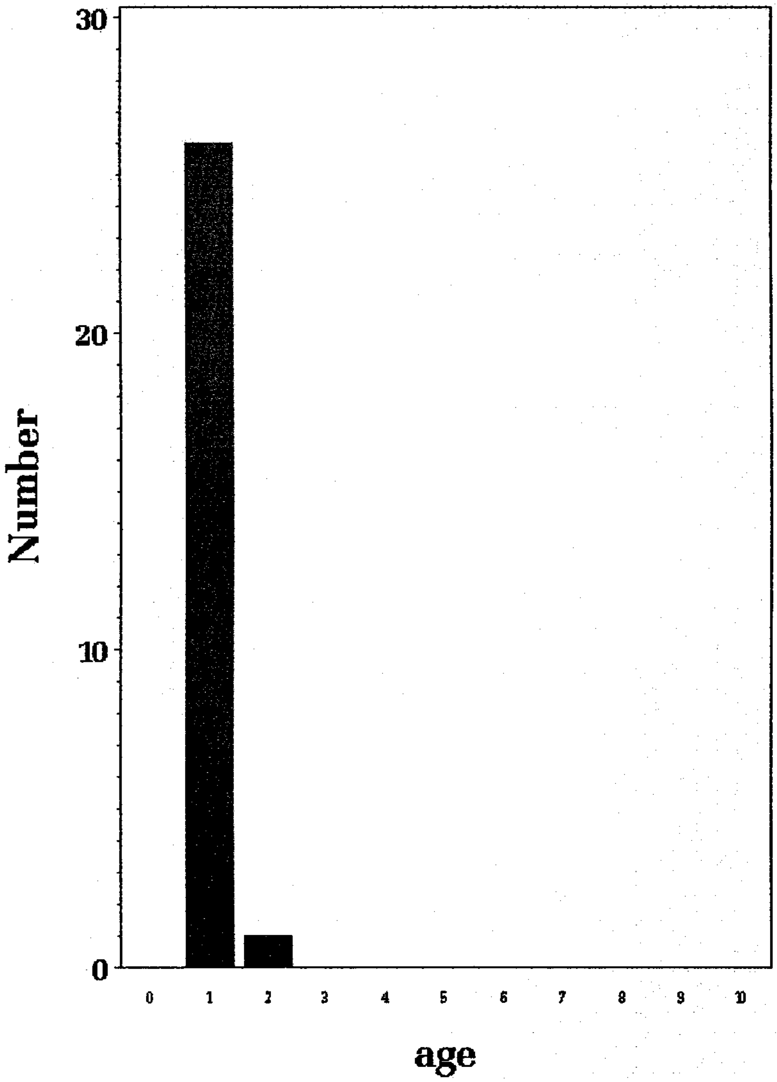


Weakfish Age Distribution

sample= 71001

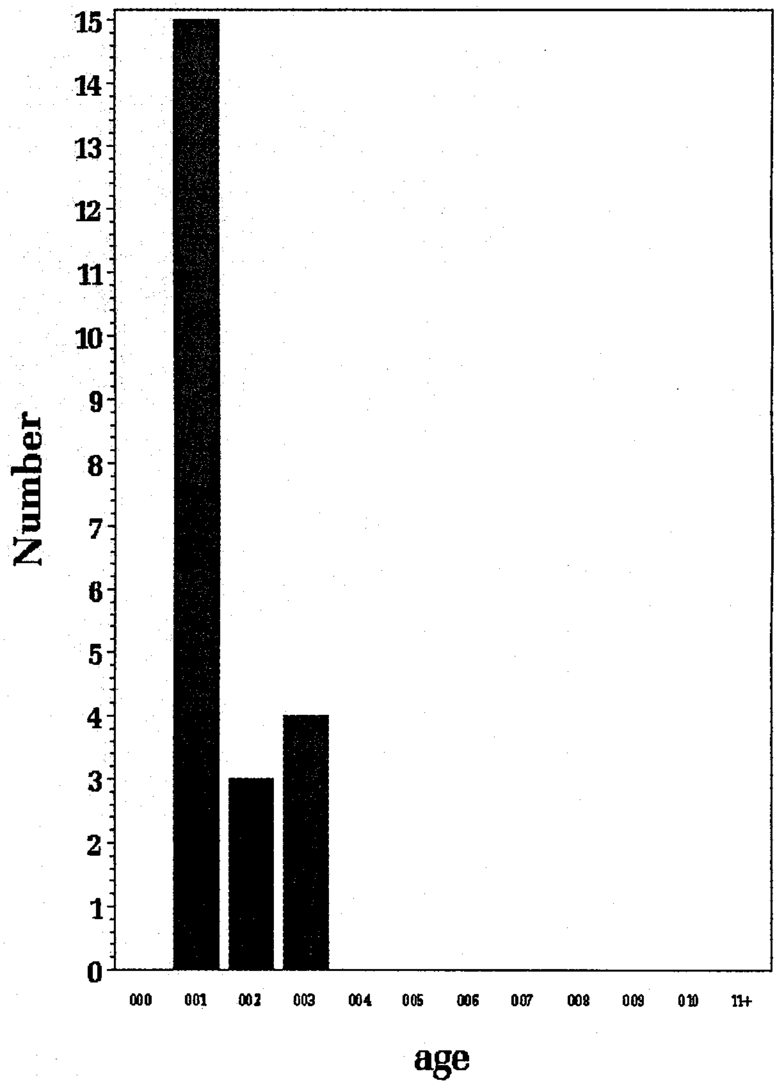
Bluefish Age Distribution

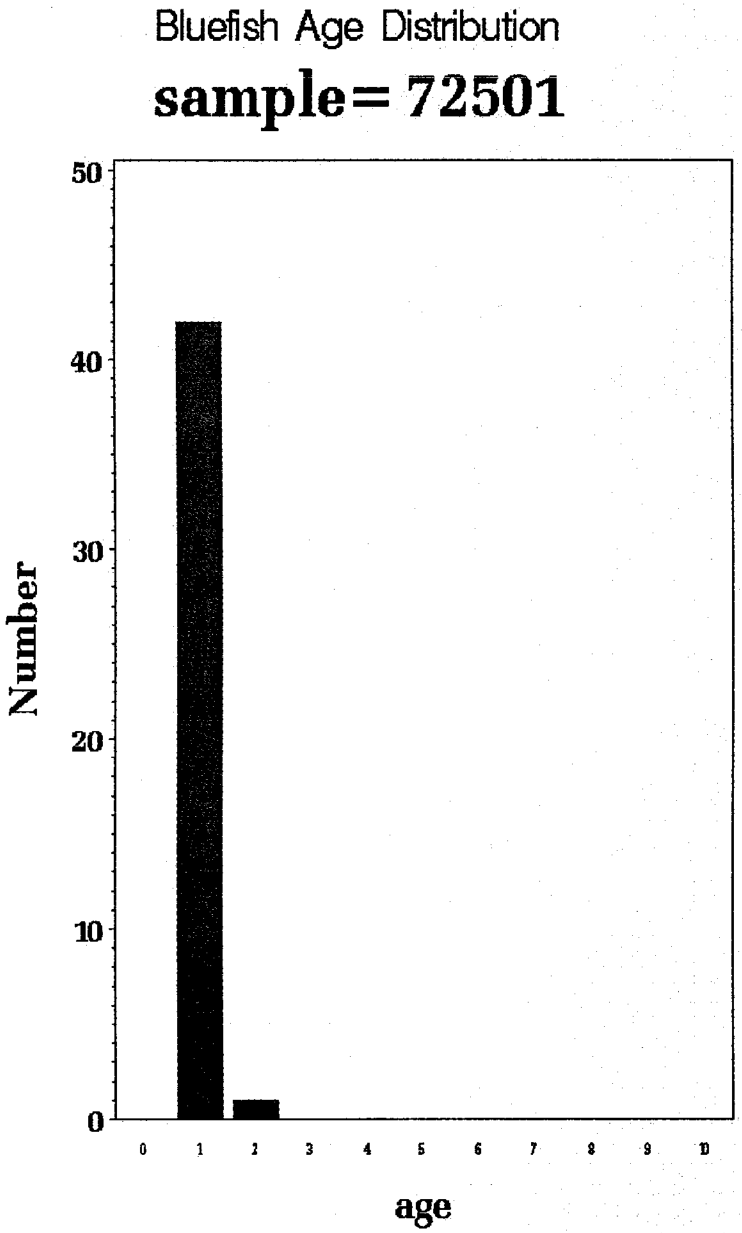
sample= 71001



Striped bass Age Distribution

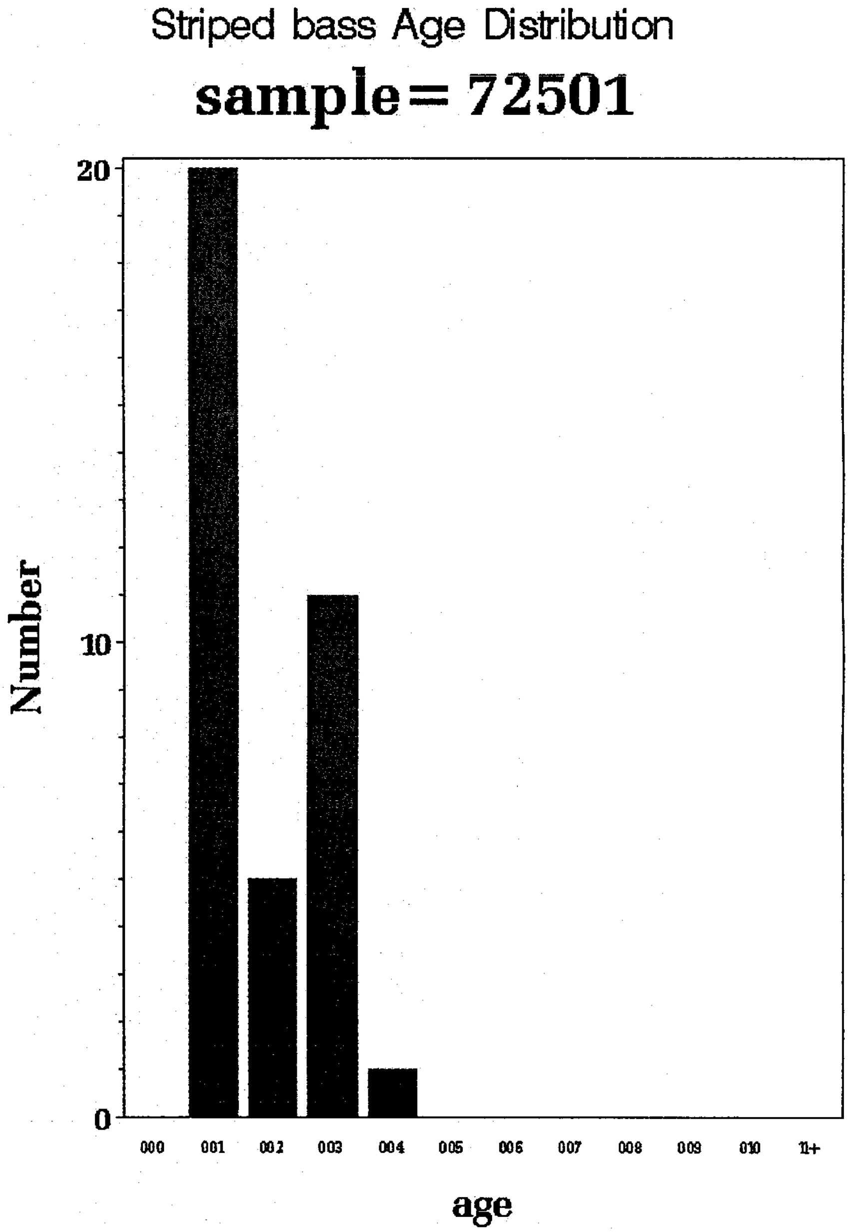
sample= 71001





Bluefish Age Distribution

sample= 72501

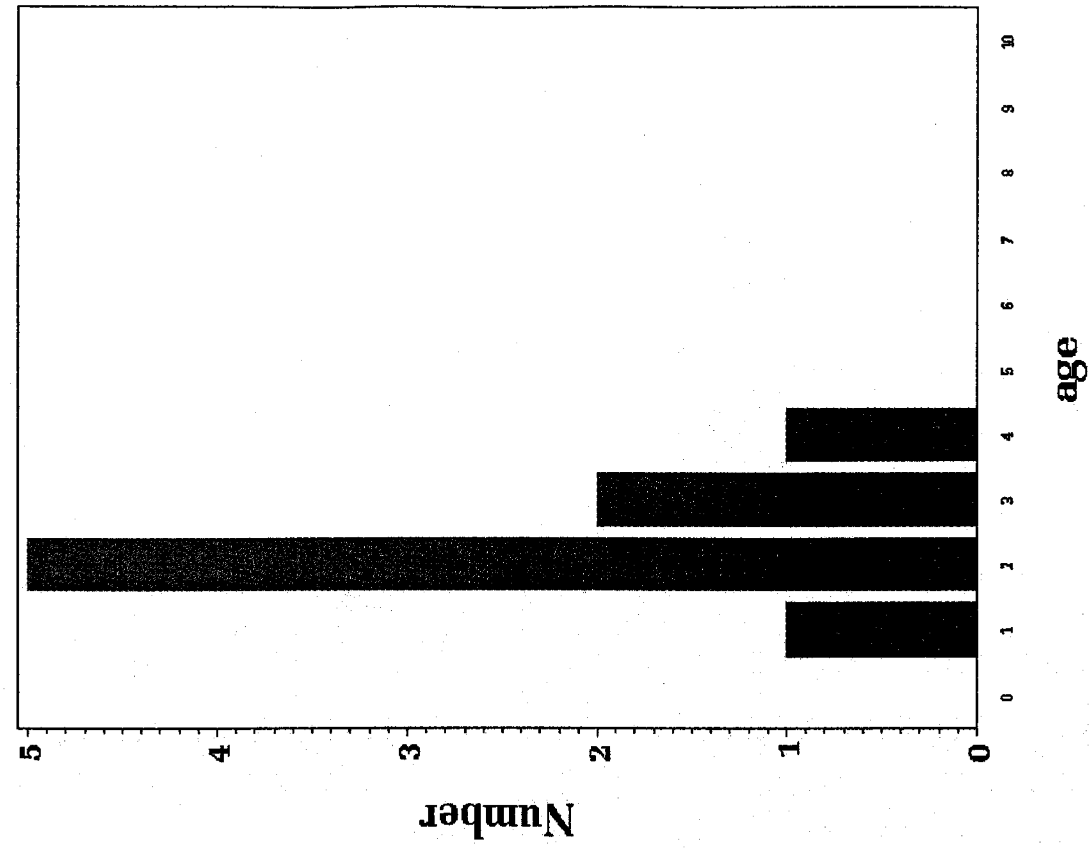


Striped bass Age Distribution

sample= 72501

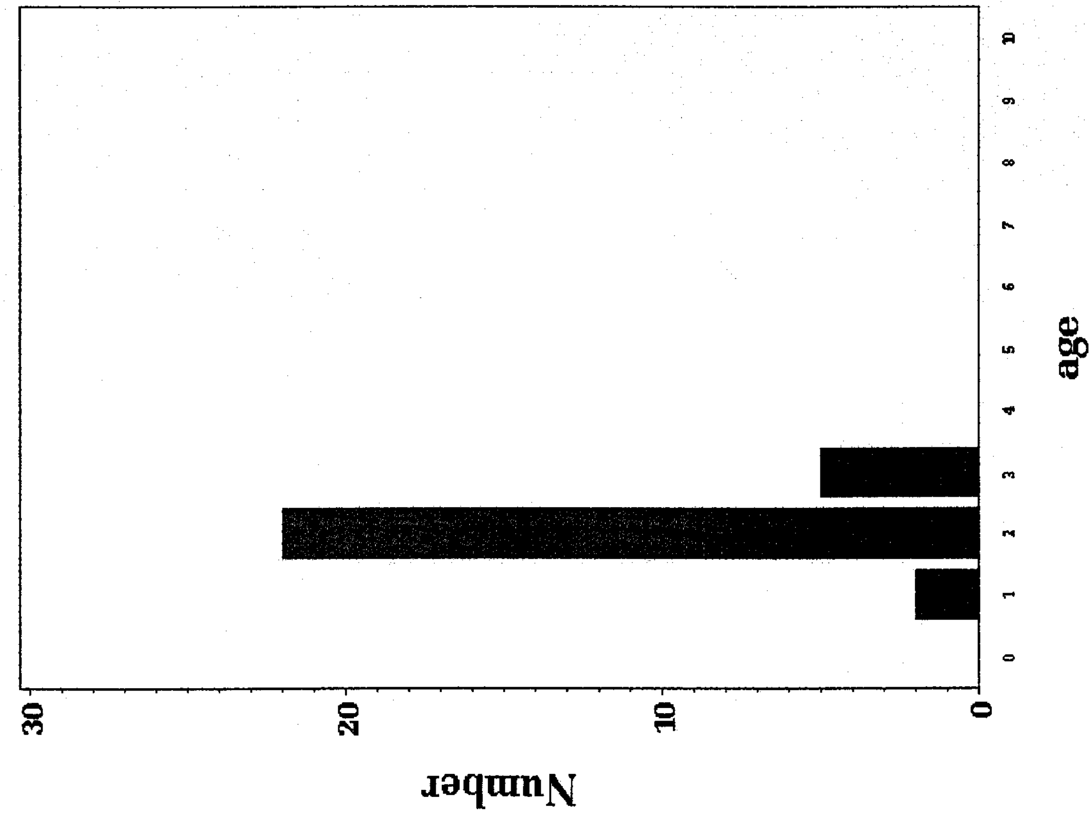
Weakfish Age Distribution

sample=82801



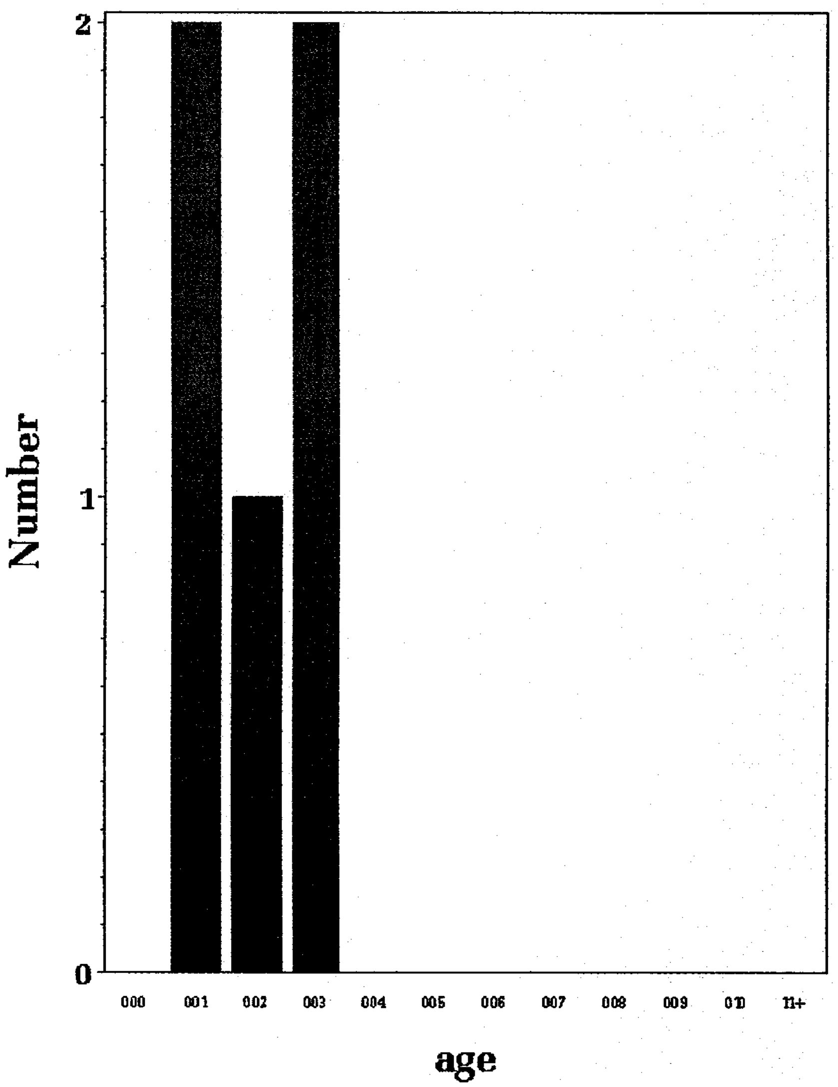
Weakfish Age Distribution

sample=72501



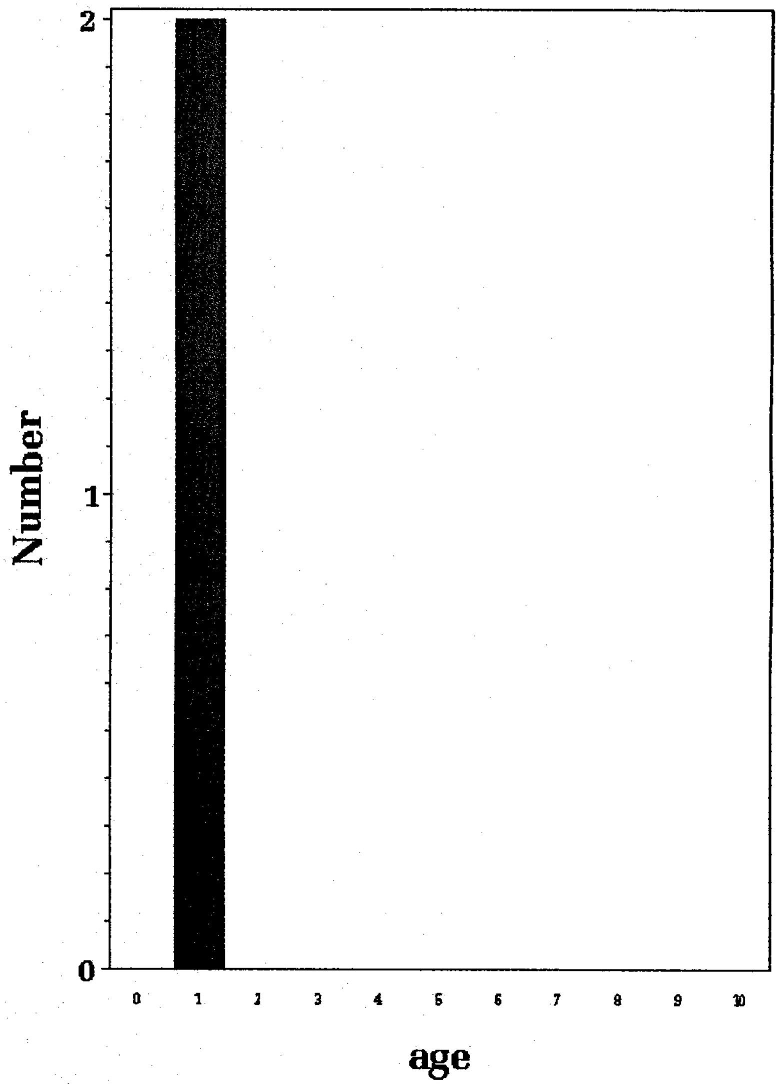
Striped bass Age Distribution

sample= 82801



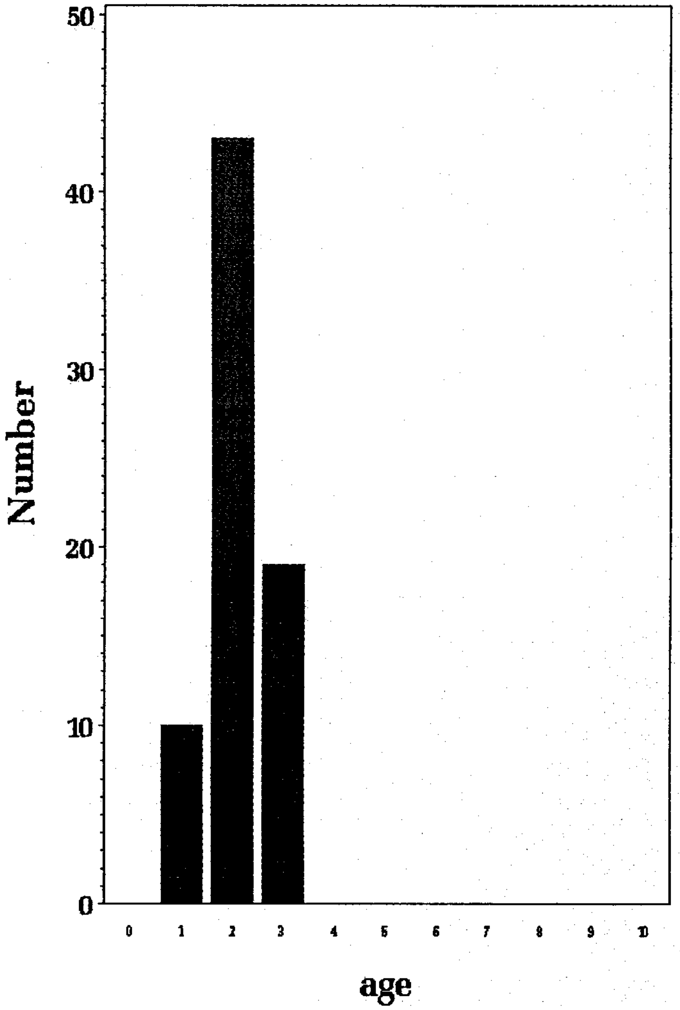
Bluefish Age Distribution

sample= 82801



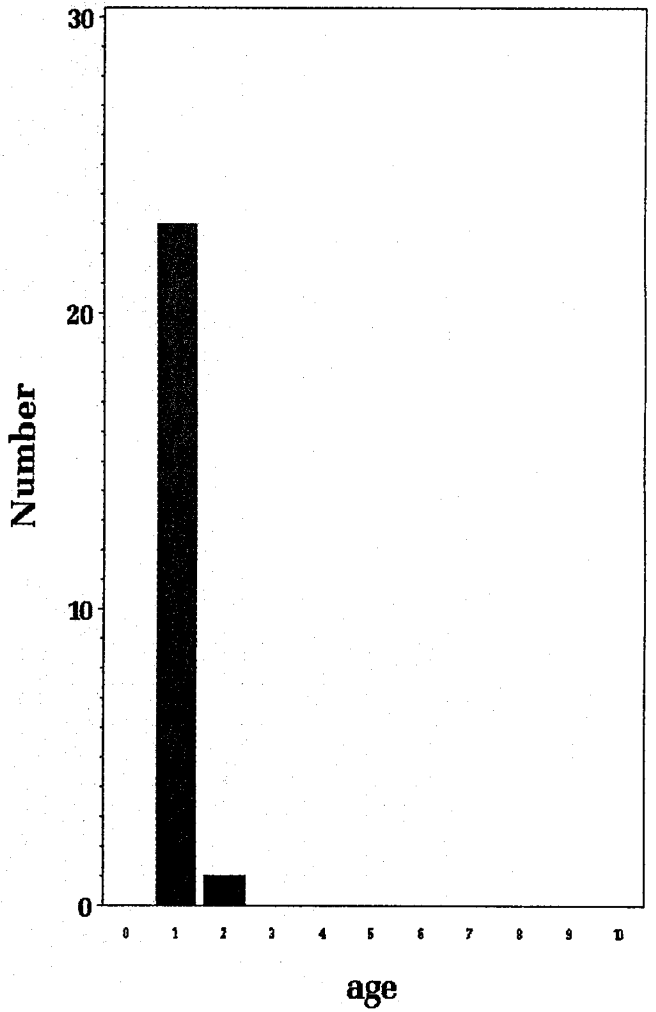
Weakfish Age Distribution

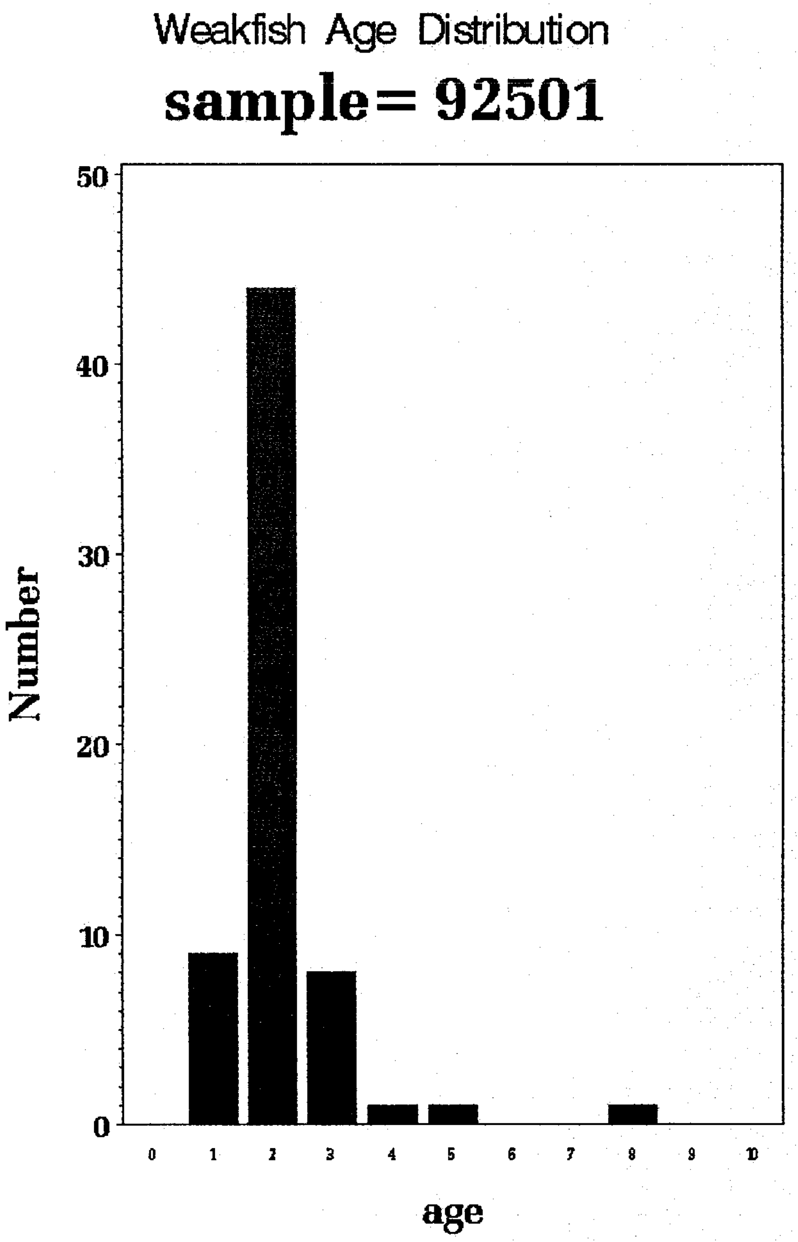
sample= 91801



Bluefish Age Distribution

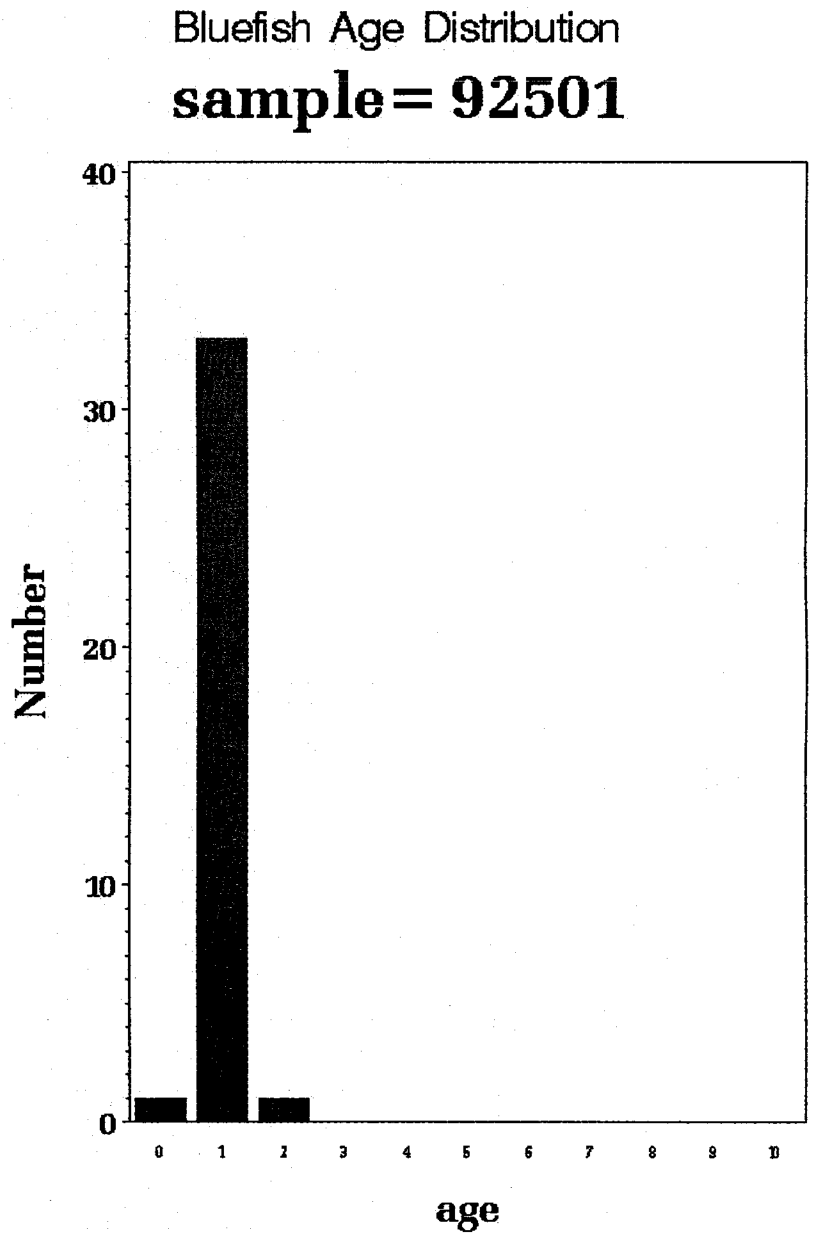
sample= 91801





Weakfish Age Distribution

sample= 92501

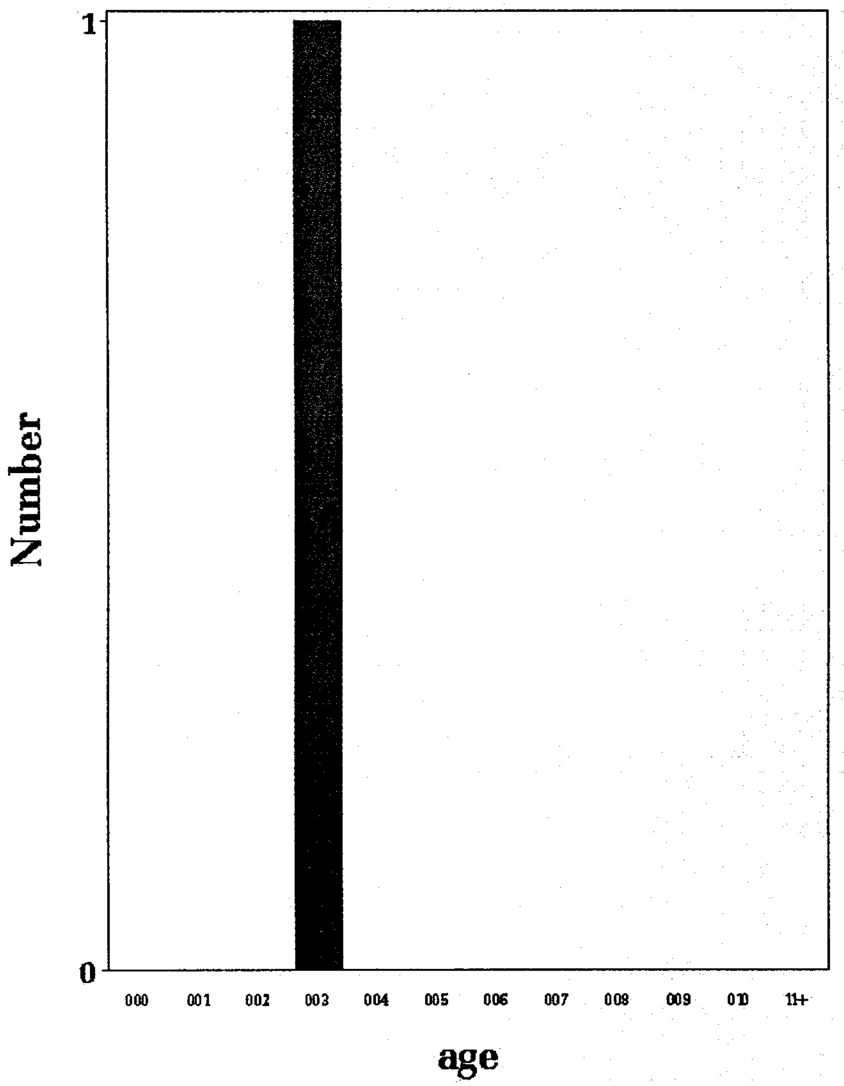


Bluefish Age Distribution

sample= 92501

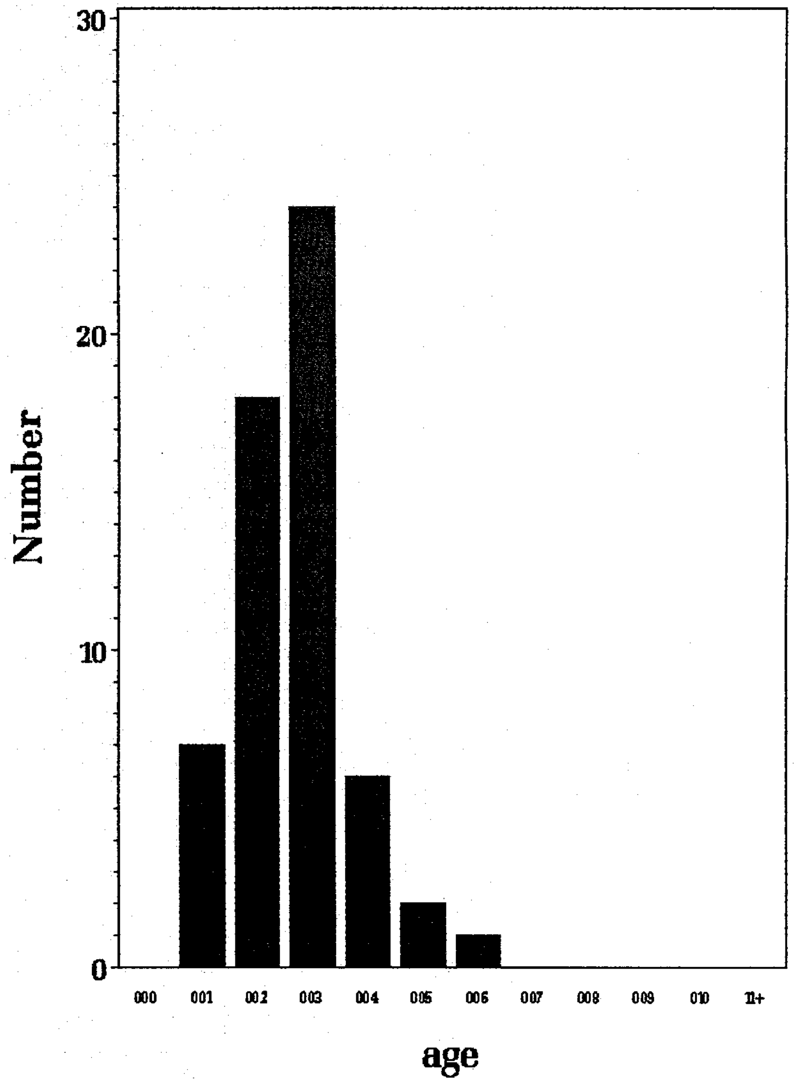
Striped bass Age Distribution

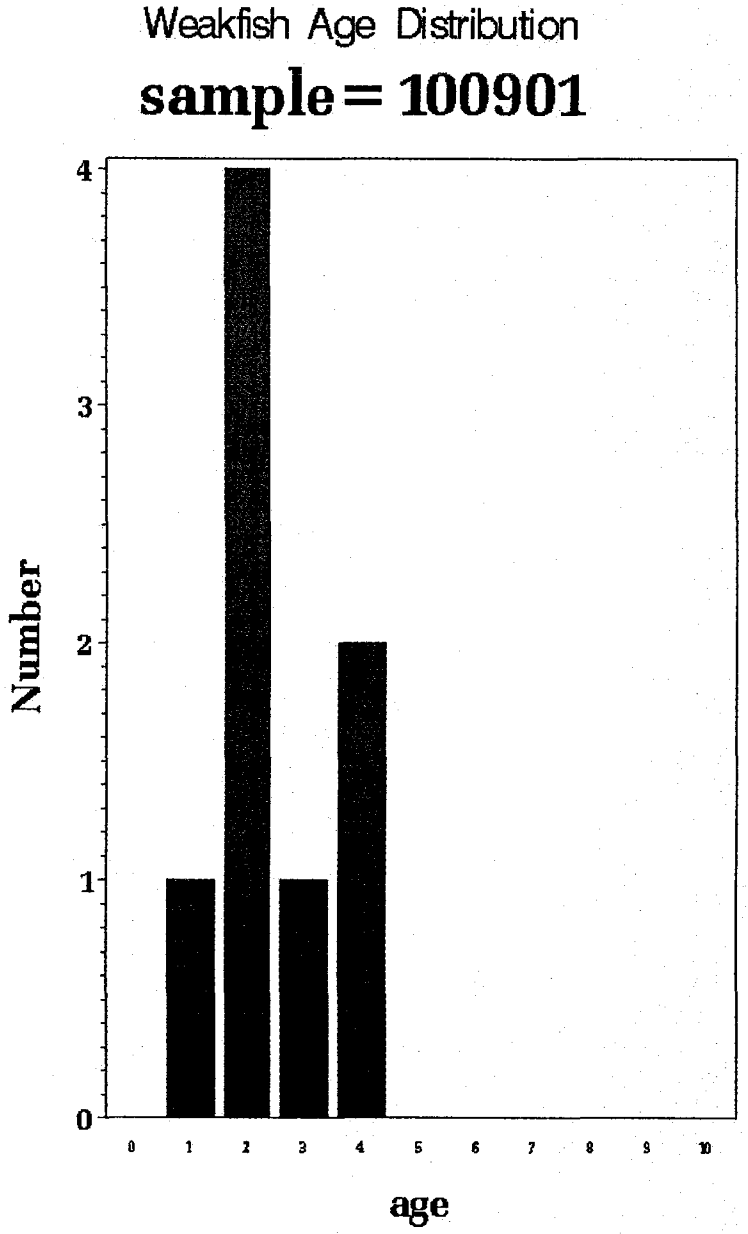
sample= 92501

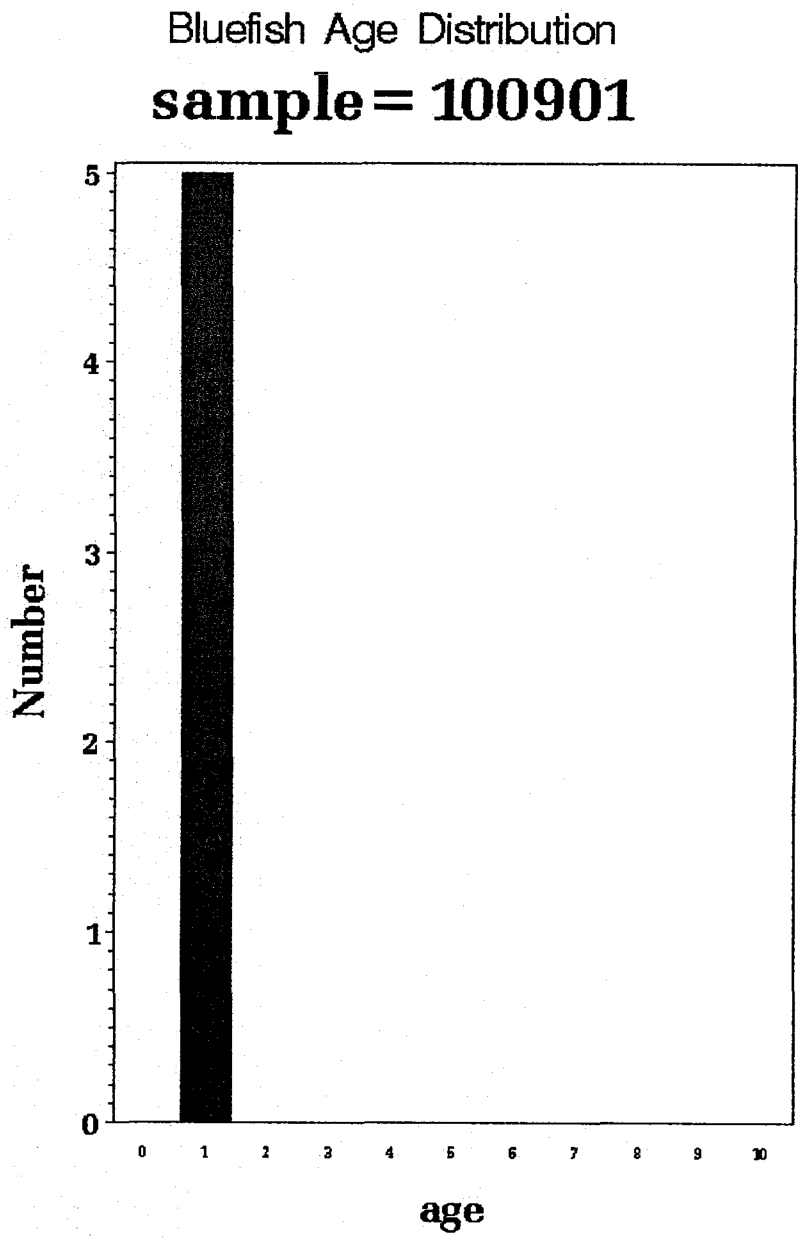


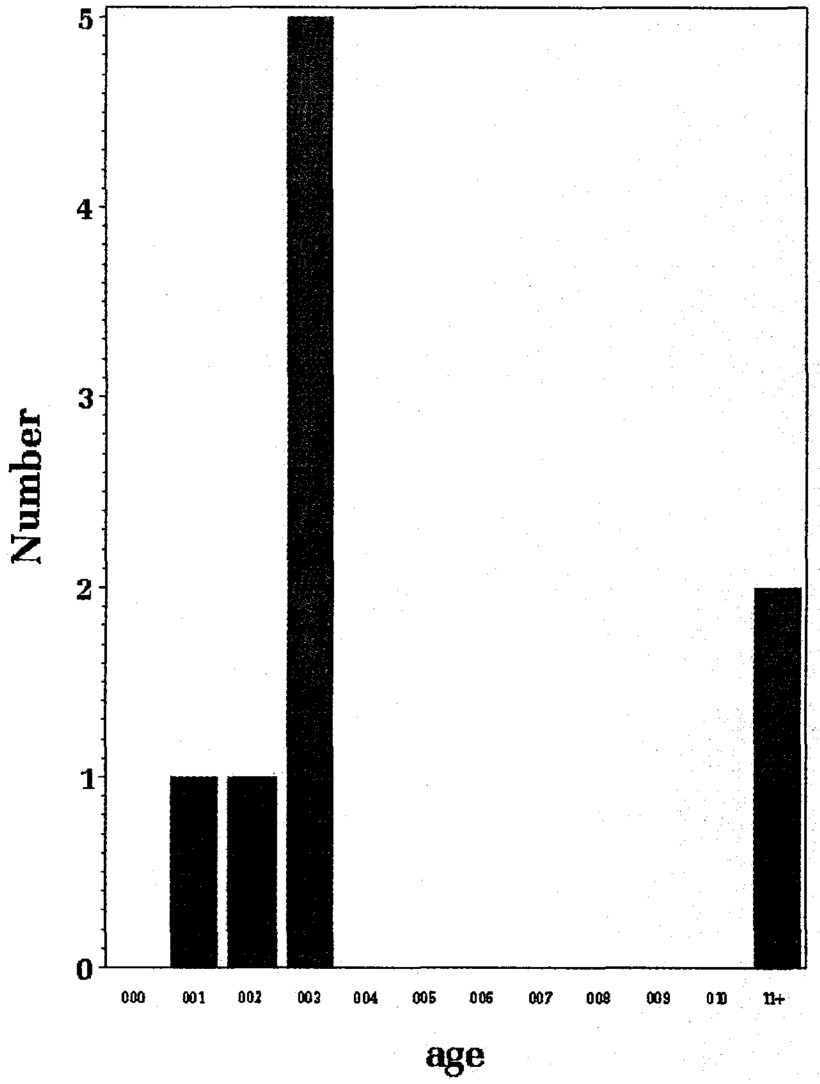
Striped bass Age Distribution

sample= 100901

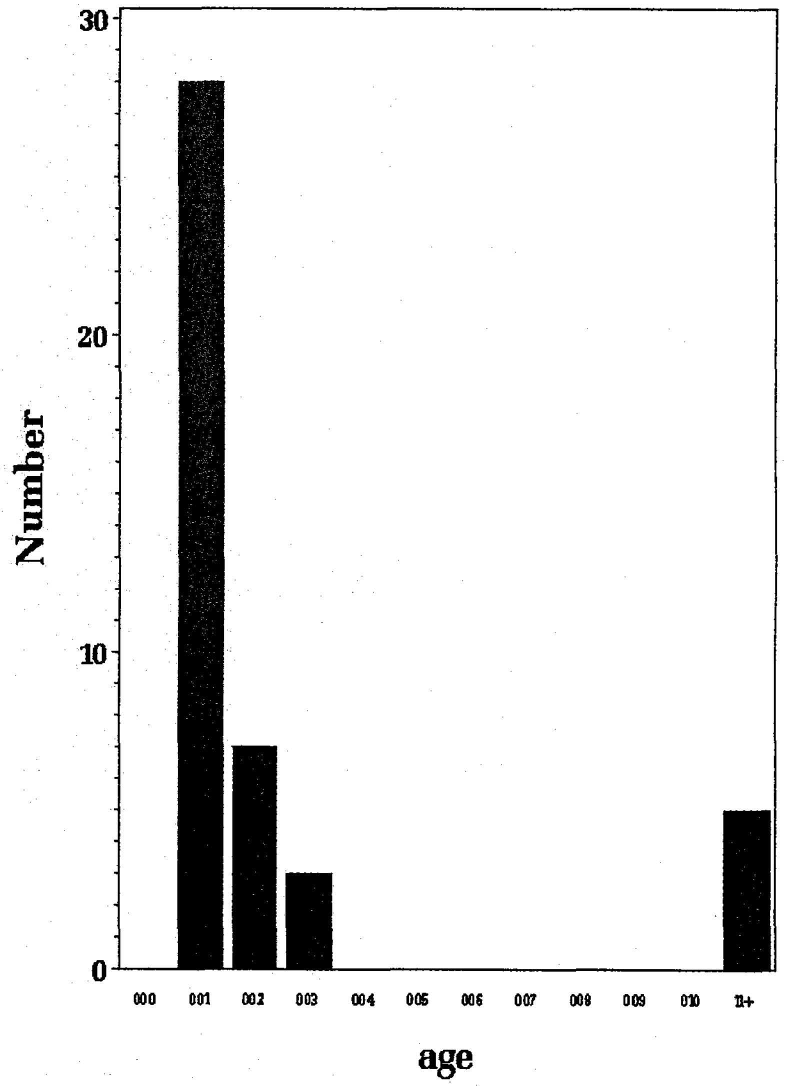



Weakfish Age Distribution
sample=100901
Number
0
1
2
3
4
age
0
1
2
3
4
5
6
7
8
9
10

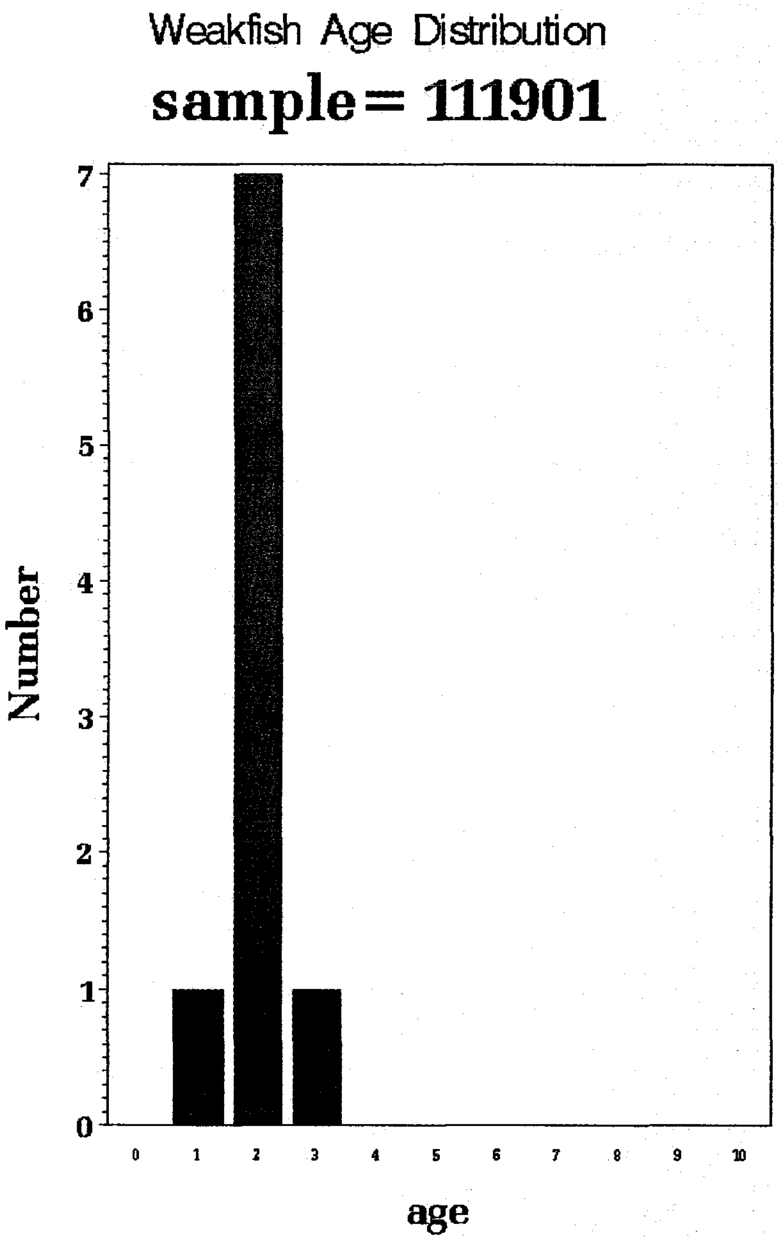

Bluefish Age Distribution
sample=100901
Number
0
1
2
3
4
5
age
0
1
2
3
4
5
6
7
8
9
10

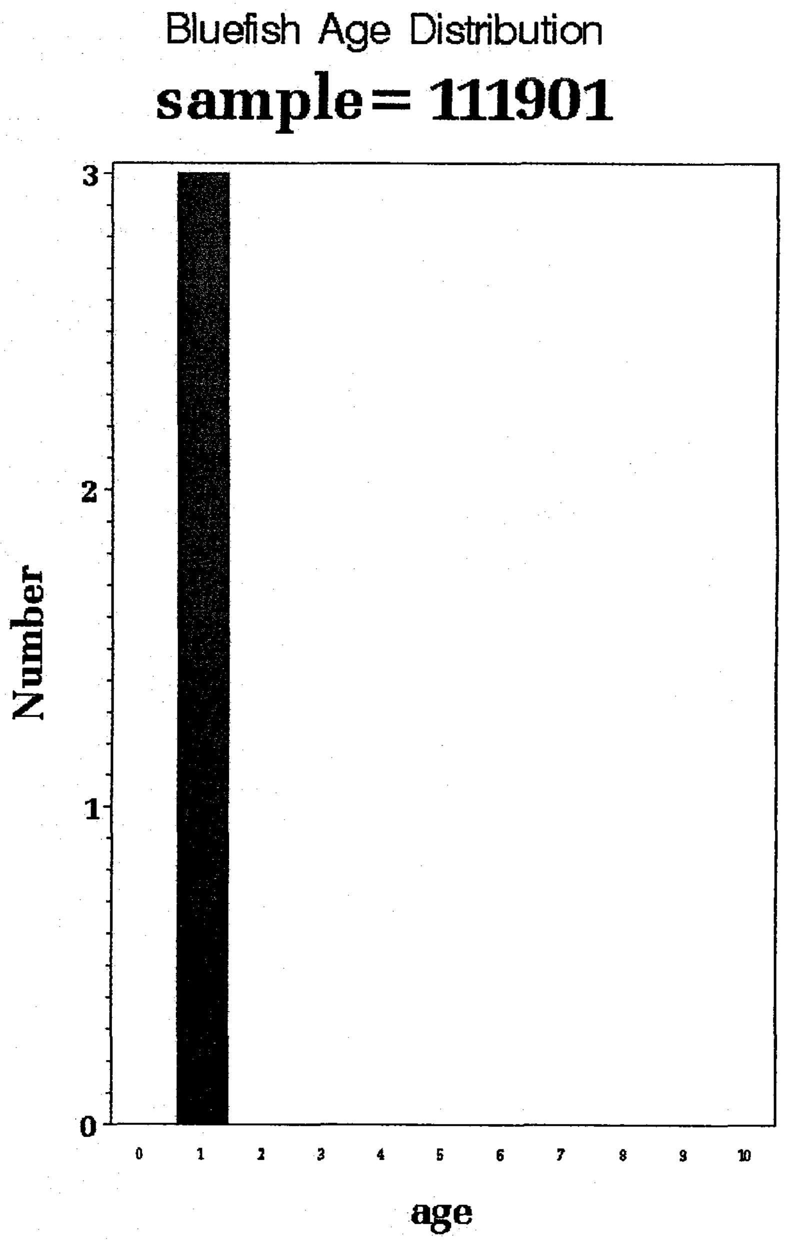

Striped bass Age Distribution

sample=103001

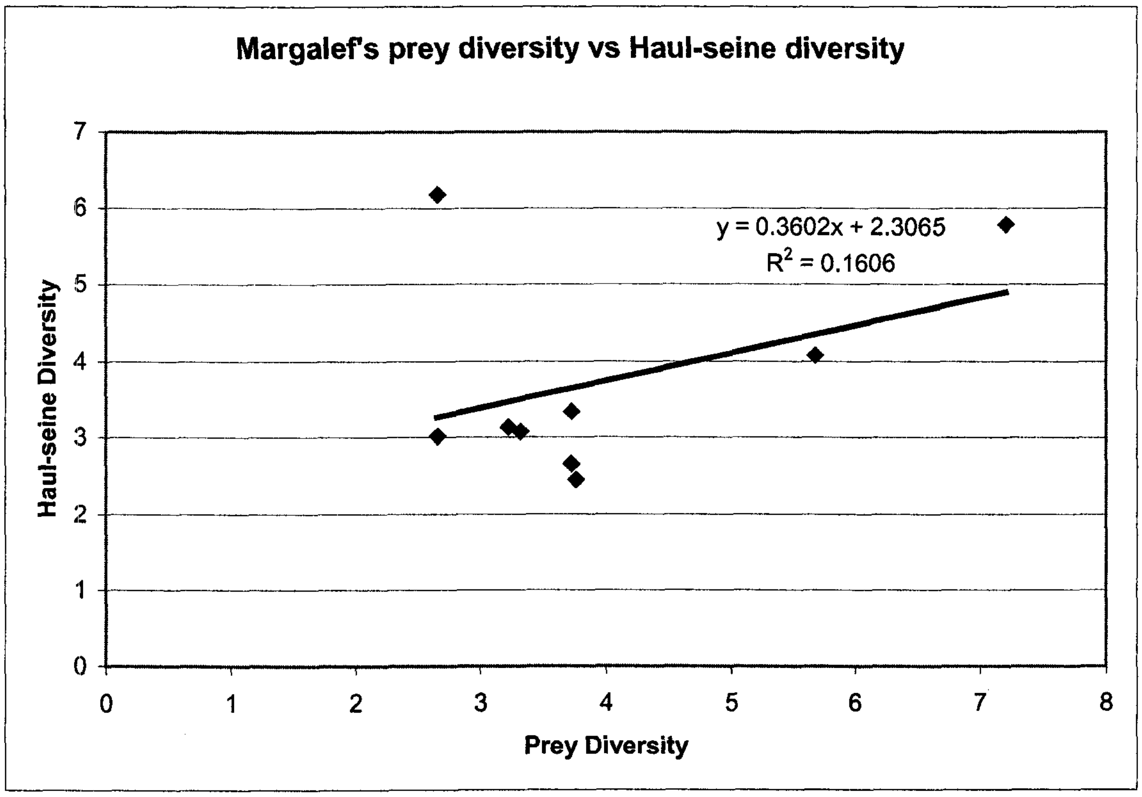

Striped bass Age Distribution

sample=111901

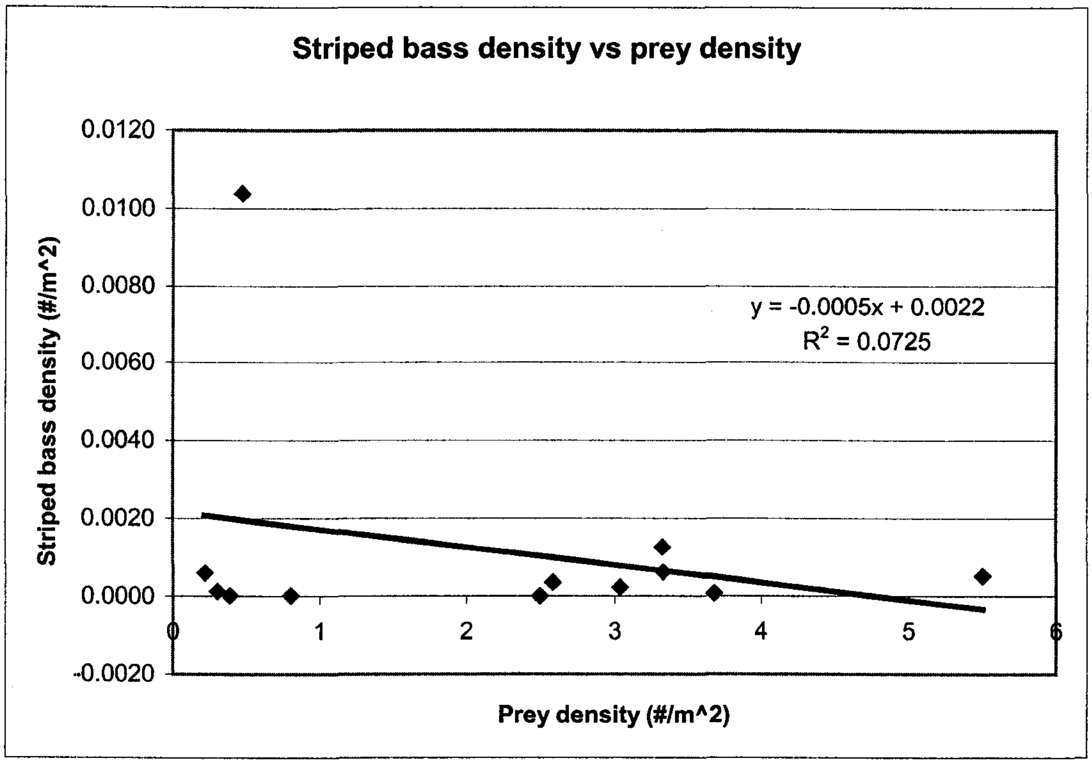

Weakfish Age Distribution
sample= 111901
Number
0
1
2
3
4
5
6
7
age
0
1
2
3
4
5
6
7
8
9
10

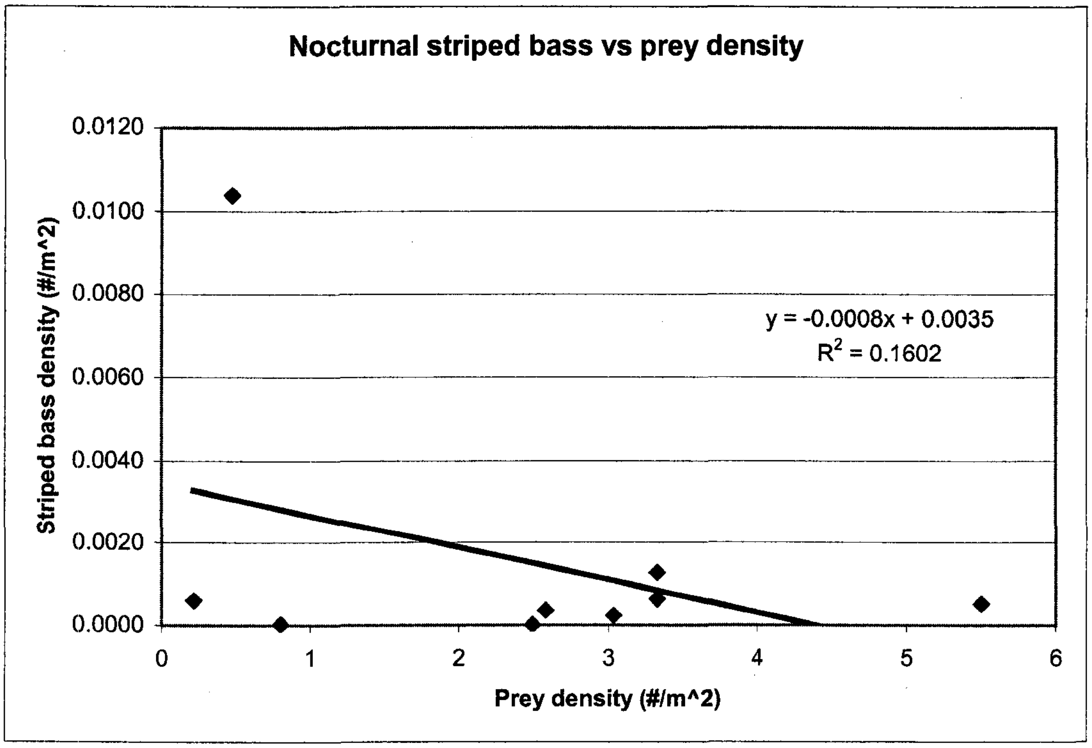

Bluefish Age Distribution
sample= 111901
Number
0
1
2
3
age
0
1
2
3
4
5
6
7
8
9
10

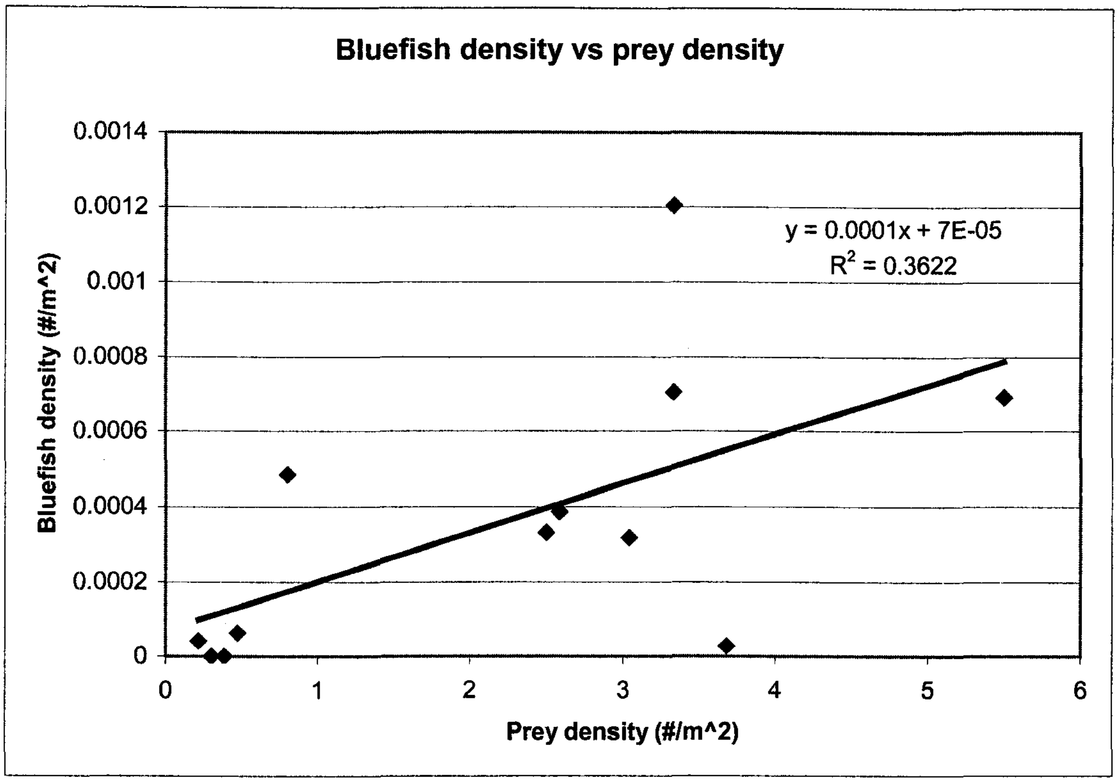
Appendix 8: This appendix contains a graph of Margalef's prey diversity vs. haul seine diversity. The two indices are not significantly related.

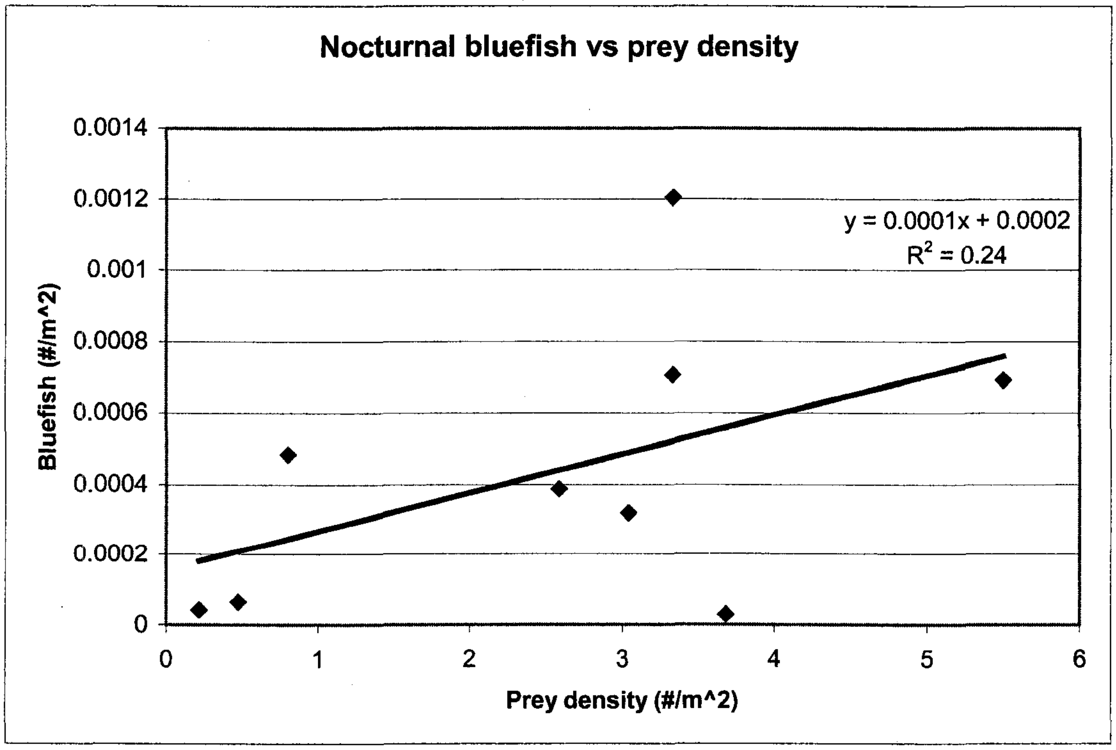


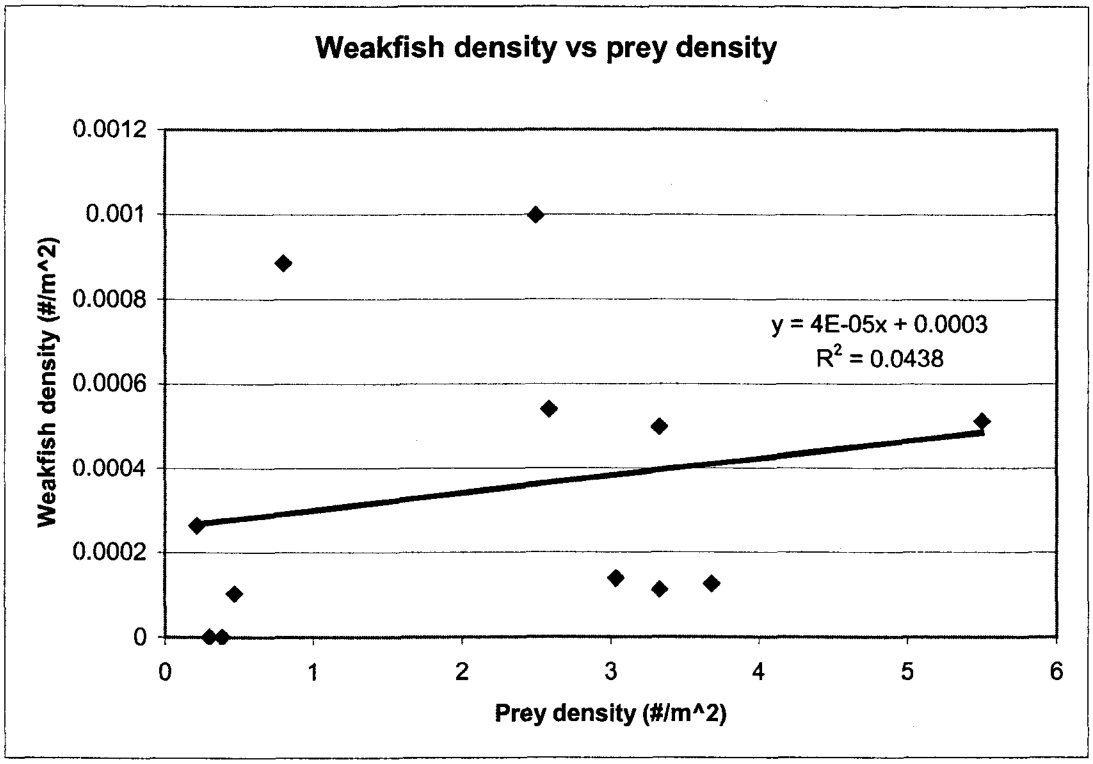
Appendix 9: This appendix contains regression analysis results between piscivores densities and summed prey densities. All samples for each fish (day and night) are examined first followed by nocturnal samples only.

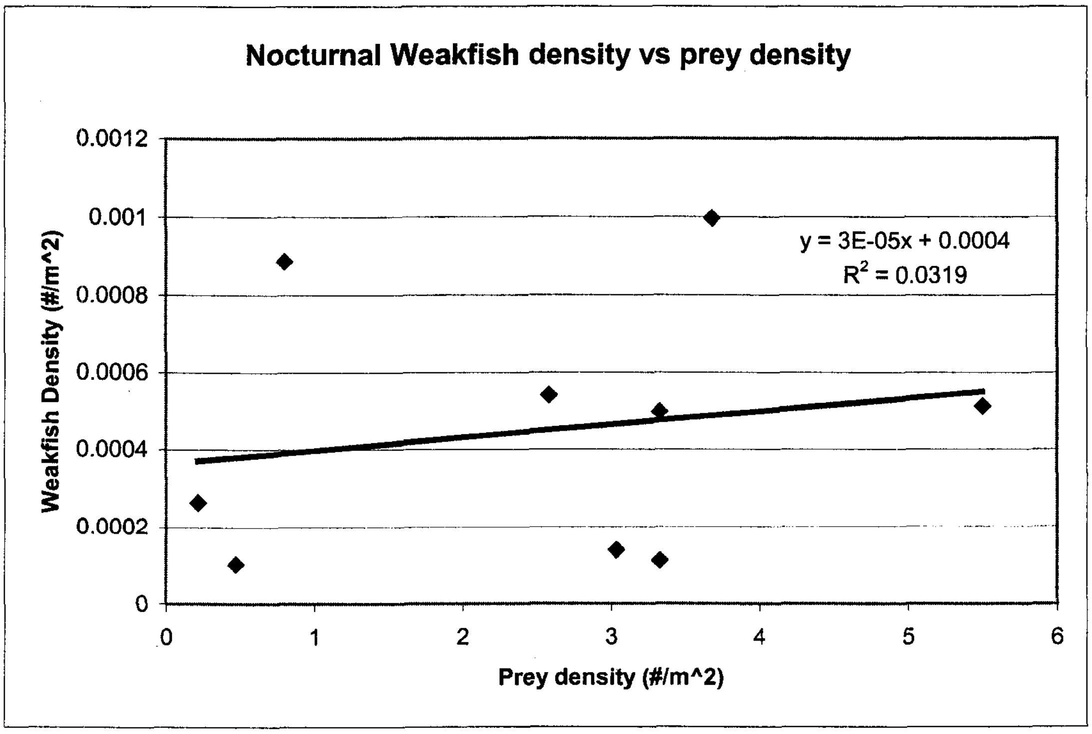





Bluefish density vs prey density
Bluefish density (#/m^2)
0.0014
0.0012
0.001
0.0008
0.0006
0.0004
0.0002
0
Prey density (#/m^2)
0
1
2
3
4
5
6
y = 0.0001x + 7E-05
R^2 = 0.3622


Nocturnal bluefish vs prey density
Bluefish (#/m^2)
0.0014
0.0012
0.001
0.0008
0.0006
0.0004
0.0002
0
Prey density (#/m^2)
0
1
2
3
4
5
6
y = 0.0001x + 0.0002
R^2 = 0.24


Weakfish density vs prey density
Weakfish density (#/m^2)
0.0012
0.001
0.0008
0.0006
0.0004
0.0002
0
0
1
2
3
4
5
6
Prey density (#/m^2)
y = 4E-05x + 0.0003
R² = 0.0438


Nocturnal Weakfish density vs prey density
Weakfish Density (#/m^2)
0.0012
0.001
0.0008
0.0006
0.0004
0.0002
0
0
1
2
3
4
5
6
Prey density (#/m^2)
y = 3E-05x + 0.0004
R² = 0.0319

Appendix 10: This appendix provides haul-seine fish assemblage comparisons with reported commercial catches and bycatch and gear impact discussions.

Haul-seine Comparisons with Commercial Fishery

Multiyear commercial haul-seine catch reports retained by the Virginia Marine Resource Commission (2003) offer the only means of assemblage structure comparison with this study's haul-seine samples. One of the intents of this study was to provide a fishery independent data set that could be use to improve our understanding of the commercial haul-seine fishery and its impacts. Establishing similar catch composition strengthens comparisons. Initially, catch composition and order of abundance appear to differ. Examination of reporting criteria and fishery mechanics offers reasonable explanations for these discrepancies.

According to commercial reports based on fish sales, croaker constituted by far the largest mass in the Virginia haul-seine fishery in 2001. Spot, gizzard shad, and weakfish followed in order of decreasing mass contributions. The top three species captured in this study mimic that of reported commercial landings in abundance but in a slightly different order (gizzard shad, croaker, spot). In species specific mass contributions catch composition varied in order (gizzard shad, croaker, striped bass, spot, bluefish, and weakfish) due to the capture of striped bass and bluefish.

In Virginia only some fish are reported species specifically separately. Therefore, reports reflect what was marketed, not what was caught. Gizzard shad caught in Virginia are not sold as bait but are exported out of state. The market is extremely small, and, thus, demand is met quickly. The lack of reporting large catches of the species simply reflects the scarcity of a market. Continued differentially large harvest and release of the species is evidenced by volunteer gear modifications that many fishermen make in order to ease the species release. In most cases buoys are left off of a portion of the pocket's top line in order to allow the side to be submersed providing release. The release method works species specifically because fishes stratify naturally within the pocket and the shad prefers the surface layer.

The discrepancies in species mass order result from the above-mentioned reporting scheme and laws governing the harvest of striped bass. Bluefish are landed in larger numbers than reporting suggest but they are sold as crab bait due to small average size, poor flesh quality, and an increased demand for fresh bait during the study season. The minimum size requirements and the individual transferable quota (ITQ) system currently being applied to striped bass harvest explain why the species is not retained by haul-seiners. In the present ITQ system each fishermen's harvest is limited by a given number of tags. To maximize profit, fishermen tag the largest fish.

Most of the striped bass that were captured during this study were small compared to what the Chesapeake's fishery is capable of supplying at other times of the year. These smaller fish if captured by a commercial operation would be released in favor of expending the tag on a much larger fish.

Given the above mentioned reporting requirements and its basis on fish sold and marketed in species categories the composition and order of abundance determined by this study mimics that captured by commercial operations. Comparisons after explanations give every indication that the study provides a reasonable likeness to current commercial harvest and techniques.

Gear impacts

Haul seining provided a consistent sampling method of large transient fishes in an ecologically important habitat on a scale that that had previously not been accomplished and was necessary to assess habitat use by highly mobile larger fishes. Its use demonstrated that the gear is relatively free of bycatch issues. Spot was the only commercially important species for which large numbers of sub-marketable fish were taken. Repeated haul-seine operation provided insight into habitat alterations that result from traditional gear operation methods and lead to the development of an alternate means of gear operation designed to prevent or at least minimize the fishery's impact on submerged aquatic vegetation (SAV) and/or other benthic habitats.

Haul-seines consist of multiple sections of seine tied or lapped together, which are used to encircle fish in shallow water. The area within the seine is gradually reduced by systematically removing sections. In order to accomplish this, the net is pulled into shallow water using the boats propeller. After each forward pull a section of net is pulled into the boat (back loaded) as the vessel is reversed in the opposite direction of the previous pull. This procedure is repeated for most of the net's sections. Given restrictive water depths propeller wash or actual contact with the substrate can disturb and/or destroy the benthic community, including SAV, during this operation. The long-term ecological impact of such disturbance is not well understood, but it seems that removal of eelgrass results in colonization by competitively inferior species (Jackson et al., 2001). Given the extent of damage done by propeller scares as evidenced by aerial photography (Orth, 2002), steps should be taken to minimize scarring and preserve seagrass coverage. This preservation initiative is strengthened by the growing evidence that such habitats are integrally linked to the production of the commercial species upon which the haul-seine and other fisheries depend.

In order to eliminate the need for backloading a hydraulic winch mechanism was mounted in a shallow draft boat. The seine was brought to shore in the traditional manner using the larger and deeper draft pull boat. The high tide during this stage will minimize prop scarring. The smaller winch boat was then moved into the shallows and anchored. Once the terminal end of the seine was fed into the winch and the seine could be fished with reduced manpower and no subsequent prop use.

The shallow draft of the winch boat also allows the rig to be repositioned during harvest as needed with minimal contact with the sea floor. This innovation offered considerable improvement over existing methods because it reduced effort and ecological impact.

Appendix 11: This appendix contains age length regressions and size divisions used to estimate piscivore ages.

	Striped bass	Bluefish	Weakfish
	Lt = 227.06*ln(age)+271.79	Lt = 914.2*(1-e^(-.32*(age- (-.36))))	Lt = 58.957 * (age) + 188.46
	Bobko, S.J., C.M. Jones, and E.M. Robillard. In Prep. Results of 2003 Virginia-Chesapeake Bay Finfish Ageing. Annual Report to the Virginia Marine Resources Commission	Robillard, E.M., S.J. Bobko, C.S. Reiss, and C.M. Jones. In Prep. Age and Growth of Bluefish in the Middle Atlantic Bight.	Bobko, S.J., C.M. Jones, and E.M. Robillard. In Prep. Results of 2003 Virginia-Chesapeake Bay Finfish Ageing. Annual Report to the Virginia Marine Resources Commission.
AGE	Total Length (mm)	Total Length (mm)	Total Length (mm)
0	#NUM!	99	188
0.5	114	220	218
1	272	323	247
1.5	364	410	277
2	429	485	306
2.5	480	548	336
3	521	602	365
3.5	556	648	395
4	587	688	424
4.5	613	721	454
5	637	750	483
5.5	659	774	513
6	679	795	542
6.5	697	812	572
7	714	827	601
7.5	729	840	631
8	744	851	660
8.5	758	861	690
9	771	868	719
9.5	783	875	749
10	795	881	778

Appendix 12. This appendix defines the benthic and pelagic prey categories used in trophic prey ecology analysis. Species specific prey or functional prey groups within categories are listed alphabetically.

Benthic prey	Pelagic prey
Atlantic croaker	anchovy spp.
American eel	Atlantic needlefish
amphipod spp.	bluefish
blue crab	gizzard shad
clam spp.	menhaden
crangon	silverside spp.
goby spp.	weakfish
isopod spp.	
juvenile shrimp spp.	
mantis shrimp	
mud crab spp.	
mummichog	
mysid spp	
penaeid spp.	
periwinkle spp.	
pipefish spp.	
paleamonetes spp.	
polychaete spp.	
sheepshead minnow	
silver perch	
skillet fish	
spot	
unknown crab spp.	

Appendix 13. This appendix contains total catch (# caught) and age assemblage data on sampled portion of catch (total sampled). Data was used to weight prey group's mean wet weights (S) in order to estimate annual diet W%.

Date	Species	# Caught	Age 0	Age 1	Age 2	Age 3	Age 3+	Age 4	Age 4+	Total # sampled	Weighted # 1	Weighted # 2	Weighted # 3	Weighted 3+	Weighted 4	Weighted 4+
25-Apr	Striped bass	1	0	0	0	0	.	0	1	1	0.00	0.00	0.00	.	0.00	1.00
10-May	Striped bass	91	0	0	30	42	.	10	4	86	0.00	31.74	44.44	.	10.58	4.23
25-May	Striped bass	16	0	4	5	6	.	0	1	16	4.00	5.00	6.00	.	0.00	1.00
12-Jun	Striped bass	45	0	3	22	19	.	1		45	3.00	22.00	19.00	.	1.00	0.00
19-Jun	Striped bass	0	0	0	0	0	.	0	0	0	0.00	0.00	0.00	.	0.00	0.00
10-Jul	Striped bass	25	0	15	3	4	.			22	17.05	3.41	4.55	.	0.00	0.00
25-Jul	Striped bass	37	0	20	5	11	.	1		37	20.00	5.00	11.00	.	1.00	0.00
28-Aug	Striped bass	5	0	2	1	2	.			5	2.00	1.00	2.00	.	0.00	0.00
18-Sep	Striped bass	0	0	0	0	0	.	0	0	0	0.00	0.00	0.00	.	0.00	0.00
25-Sep	Striped bass	1	0			1	.			1	0.00	0.00	1.00	.	0.00	0.00
9-Oct	Striped bass	750	0	7	18	24	.	6	3	58	90.52	232.76	310.34	.	77.59	38.79
19-Nov	Striped bass	44	0	28	8	3	.	0	5	44	28.00	8.00	3.00	.	0.00	5.00
10-May	Bluefish	87	0	52	35	.	.	.	.	87	52.00	35.00	.	.	.	.
25-May	Bluefish	23	0	5	9	.	.	.	.	14	8.21	14.79	.	.	.	.
12-Jun	Bluefish	51	0	42	6	.	.	.	.	48	44.63	6.38	.	.	.	.
19-Jun	Bluefish	4	0	4	0	.	.	.	.	4	0.00	0.00	.	.	.	.
10-Jul	Bluefish	28	0	26	1	.	.	.	.	27	26.96	1.04	.	.	.	.
25-Jul	Bluefish	50	0	44	1	.	.	.	.	45	48.89	1.11	.	.	.	.
28-Aug	Bluefish	8	0	8	0	.	.	.	.	8	8.00	0.00	.	.	.	.
18-Sep	Bluefish	24	0	23	1	.	.	.	.	24	23.00	1.00	.	.	.	.
25-Sep	Bluefish	35	1	32	1	.	.	.	.	34	32.94	1.03	.	.	.	.
9-Oct	Bluefish	5	0	5	0	.	.	.	.	5	5.00	0.00	.	.	.	.

19-Nov	Bluefish	3	0	2	0	.	.	.	.	2	3.00	0.00	.	.	.	.
10-May	Weakfish	36	0	0	19	11	6		.	36	0.00	19.00	11.00	6.00	.	.
25-May	Weakfish	10	0	2	6	1	0	.	.	9	2.22	6.67	1.11	0.00	.	.
12-Jun	Weakfish	8	0	3	2	2	0	.	.	7	3.43	2.29	2.29	0.00	.	.
19-Jun	Weakfish	0	0	0	0	0	0	.	.	0	0.00	0.00		0.00	.	.
10-Jul	Weakfish	39	0	1	36	14	0	.	.	51	0.76	27.53	10.71	0.00	.	.
25-Jul	Weakfish	37	0	2	22	5	0	.	.	29	2.55	28.07	6.38	0.00	.	.
28-Aug	Weakfish	9	0	1	5	2	1	.	.	9	1.00	5.00	2.00	1.00	.	.
18-Sep	Weakfish	72	0	10	42	20	0	.	.	72	10.00	42.00	20.00	0.00	.	.
25-Sep	Weakfish	64	0	9	44	8	3	.	.	64	9.00	44.00	8.00	3.00	.	.
9-Oct	Weakfish	8	0	1	4	1	2	.	.	8	1.00	4.00	1.00	2.00	.	.
19-Nov	Weakfish	19	0	1	8	1	0	.	.	10	1.90	15.20	1.90	0.00	.	.

Appendix 14. This appendix contains all indices calculated for striped bass, bluefish and weakfish. Diel samples (dates italicized) are listed but were not included in further analysis due to reduced sample abundances. Data is listed by species then age then sample date.

Date	Predator	Age	# examined	Prey	S (gm/fish)	G. F. I. (gm prey /gm predator)	W%	O%	N%	IRI	%IRI
6/12/2001	Striped bass	1	3	silver perch	S (gm/fish)	0.0035414	44.4	33.3	2.0	0.15	17.8
6/12/2001	Striped bass	1	3	paleamonetes spp.	0.80	0.0022134	27.8	66.7	32.7	0.40	46.4
6/12/2001	Striped bass	1	3	anchovy spp.	0.50	0.0007378	9.3	33.3	2.0	0.04	4.3
6/12/2001	Striped bass	1	3	unknown	0.17	0.0005902	7.4	33.3	2.0	0.03	3.6
6/12/2001	Striped bass	1	3	amphipod spp.	0.13	0.0002951	3.7	33.3	22.4	0.09	10.0
6/12/2001	Striped bass	1	3	isopodspp.	0.07	0.0002951	3.7	33.3	34.7	0.13	14.7
6/12/2001	Striped bass	1	3	polychaete spp.	0.07	0.0002951	3.7	33.3	4.1	0.03	3.0
7/10/2001	Striped bass	1	10	blue crab	0.07	0.0199370	83.2	50.0	4.7	0.44	76.4
7/10/2001	Striped bass	1	10	amphipod spp.	4.11	0.0016477	6.9	10.0	92.2	0.10	17.2
7/10/2001	Striped bass	1	10	paleamonetes spp.	0.34	0.0010661	4.4	50.0	1.4	0.03	5.1
7/10/2001	Striped bass	1	10	mummichog	0.22	0.0007754	3.2	10.0	0.2	0.00	0.6
7/10/2001	Striped bass	1	10	goby spp.	0.16	0.0004846	2.0	10.0	0.2	0.00	0.4
7/10/2001	Striped bass	1	10	isopod spp.	0.10	0.0000582	0.2	10.0	1.4	0.00	0.3
7/25/2001	Striped bass	1	13	paleamonetes spp.	0.01	0.0027913	37.9	23.1	42.6	0.19	47.0
7/25/2001	Striped bass	1	13	silverside spp.	0.68	0.0024463	33.2	23.1	27.8	0.14	35.6
7/25/2001	Striped bass	1	13	silver perch	0.60	0.0006273	8.5	15.4	3.7	0.02	4.8
7/25/2001	Striped bass	1	13	mummichog	0.15	0.0004704	6.4	7.7	1.9	0.01	1.6
7/25/2001	Striped bass	1	13	crangon	0.12	0.0004077	5.5	15.4	5.6	0.02	4.3
7/25/2001	Striped bass	1	13	sheepshead minnow	0.10	0.0002823	3.8	7.7	5.6	0.01	1.8
7/25/2001	Striped bass	1	13	unknown	0.07	0.0001568	2.1	15.4	3.7	0.01	2.3
7/25/2001	Striped bass	1	13	anchovy spp.	0.04	0.0000627	0.9	7.7	1.9	0.00	0.5
7/25/2001	Striped bass	1	13	scales	0.02	0.0000627	0.9	7.7	5.6	0.00	1.2
7/25/2001	Striped bass	1	13	unknown fish	0.02	0.0000157	0.2	7.7	1.9	0.00	0.4

7/25/2001	Striped bass	1	13	SAV	0.00	0.0000157	0.2	7.7	1.9	0.00	0.4
8/28/2001	Striped bass	1	2	silverside spp.	0.00	0.0059487	100.0	100.0	100.0	2.00	100.0
10/9/2001	Striped bass	1	7	blue crab	1.45	0.0007369	73.7	14.3	20.0	0.13	46.8
10/9/2001	Striped bass	1	7	anchovy spp.	0.20	0.0002632	26.3	14.3	80.0	0.15	53.2
11/19/2001	Striped bass	1	12	crangon	0.07	0.0025838	79.8	50.0	63.3	0.72	88.5
11/19/2001	Striped bass	1	12	anchovy spp.	0.92	0.0003971	12.3	16.7	30.6	0.07	8.8
11/19/2001	Striped bass	1	12	unknown fish	0.14	0.0002336	7.2	16.7	4.1	0.02	2.3
11/19/2001	Striped bass	1	12	SAV	0.08	0.0000234	0.7	8.3	2.0	0.00	0.3
5/10/2001	Striped bass	2	6	polychaete spp.	0.01	0.0087524	91.4	100.0	98.7	1.90	97.5
5/10/2001	Striped bass	2	6	blue crab	7.60	0.0008253	8.6	50.0	1.3	0.05	2.6
5/25/2001	Striped bass	2	1	polychaete spp.	0.72	0.0008000	46.2	100.0	72.7	1.19	59.5
5/25/2001	Striped bass	2	1	blue crab	0.80	0.0007000	40.5	100.0	9.1	0.50	24.8
5/25/2001	Striped bass	2	1	paleamonetes spp.	0.70	0.0002000	11.6	100.0	9.1	0.21	10.3
5/25/2001	Striped bass	2	1	SAV	0.20	0.0000300	1.7	100.0	9.1	0.11	5.4
6/12/2001	Striped bass	2	10	blue crab	0.03	0.0043537	92.0	90.0	90.7	1.64	97.2
6/12/2001	Striped bass	2	10	paleamonetes spp.	4.16	0.0003663	7.7	30.0	7.0	0.04	2.6
6/12/2001	Striped bass	2	10	SAV	0.35	0.0000105	0.2	10.0	2.3	0.00	0.2
7/10/2001	Striped bass	2	5	silverside spp.	0.01	0.0031483	99.3	20.0	93.3	0.39	96.3
7/10/2001	Striped bass	2	5	SAV	2.80	0.0000225	0.7	20.0	6.7	0.01	3.7
7/25/2001	Striped bass	2	3	silver perch	0.02	0.0002768	44.4	33.3	11.1	0.19	23.8
7/25/2001	Striped bass	2	3	blue crab	0.27	0.0002422	38.8	33.3	11.1	0.17	21.4
7/25/2001	Striped bass	2	3	SAV	0.23	0.0000692	11.1	66.7	22.2	0.22	28.6
7/25/2001	Striped bass	2	3	rock	0.07	0.0000346	5.5	33.3	11.1	0.06	7.1
7/25/2001	Striped bass	2	3	scales	0.03	0.0000007	0.1	33.3	44.4	0.15	19.1
8/28/2001	Striped bass	2	1	unknown fish	0.00	0.0027027	93.3	100.0	33.3	1.27	63.3
8/28/2001	Striped bass	2	1	SAV	0.70	0.0001931	6.7	100.0	66.7	0.73	36.7
10/9/2001	Striped bass	2	18	blue crab	0.05	0.0054332	61.5	44.4	66.7	0.57	31.8
10/9/2001	Striped bass	2	18	spot	4.52	0.0015685	17.8	5.6	3.0	0.01	0.6
10/9/2001	Striped bass	2	18	silver perch	1.31	0.0012749	14.4	16.7	9.1	0.04	2.2
10/9/2001	Striped bass	2	18	mummichog	1.06	0.0003004	3.4	5.6	3.0	0.00	0.2

10/9/2001	Striped bass	2	18	periwinkle spp.	0.25	0.0001869	2.1	11.1	6.1	0.01	0.5
10/9/2001	Striped bass	2	18	pipefish spp.	0.16	0.0000400	0.5	11.1	6.1	0.92	51.2
10/9/2001	Striped bass	2	18	macro algae	0.03	0.0000200	0.2	5.6	3.0	0.00	0.1
10/9/2001	Striped bass	2	18	unknown fish	0.02	0.0000067	0.1	5.6	3.0	0.00	0.1
11/19/2001	Striped bass	2	6	blue crab	0.01	0.0014955	82.8	33.3	84.2	0.56	91.0
11/19/2001	Striped bass	2	6	polychaete spp.	0.88	0.0001975	10.9	16.7	5.3	0.03	4.4
11/19/2001	Striped bass	2	6	SAV	0.12	0.0000564	3.1	16.7	5.3	0.01	2.3
11/19/2001	Striped bass	2	6	unknown fish	0.03	0.0000564	3.1	16.7	5.3	0.01	2.3
5/10/2001	Striped bass	3	7	blue crab	0.03	0.0056600	63.8	85.7	10.2	0.63	48.7
5/10/2001	Striped bass	3	7	polychaete spp.	8.73	0.0022325	25.2	57.1	87.6	0.64	49.5
5/10/2001	Striped bass	3	7	spartina spp.	3.44	0.0002964	3.3	14.3	0.4	0.01	0.4
5/10/2001	Striped bass	3	7	macro algae	0.46	0.0002594	2.9	14.3	0.4	0.00	0.4
5/10/2001	Striped bass	3	7	pipefish	0.40	0.0002501	2.8	28.6	0.7	0.01	0.8
5/10/2001	Striped bass	3	7	SAV	0.39	0.0000926	1.0	14.3	0.4	0.00	0.2
5/10/2001	Striped bass	3	7	mud crab	0.14	0.0000834	0.9	14.3	0.4	0.00	0.1
5/25/2001	Striped bass	3	2	blue crab	0.13	0.0111621	93.0	100.0	78.0	1.71	92.2
5/25/2001	Striped bass	3	2	paleamonetes spp.	14.60	0.0004587	3.8	50.0	6.8	0.05	2.9
5/25/2001	Striped bass	3	2	polychaete spp.	0.60	0.0003058	2.5	50.0	13.6	0.08	4.3
5/25/2001	Striped bass	3	2	SAV	0.40	0.0000765	0.6	50.0	1.7	0.01	0.6
6/12/2001	Striped bass	3	8	blue crab	0.10	0.0093526	100.0	87.5	100.0	1.75	100.0
7/25/2001	Striped bass	3	8	blue crab	13.04	0.0023170	93.1	75.0	52.9	1.10	89.2
7/25/2001	Striped bass	3	8	shell	3.38	0.0001047	4.2	25.0	11.8	0.04	3.3
7/25/2001	Striped bass	3	8	unknown fish	0.15	0.0000343	1.4	12.5	5.9	0.01	0.7
7/25/2001	Striped bass	3	8	macro algae	0.05	0.0000150	0.6	37.5	17.6	0.07	5.6
7/25/2001	Striped bass	3	8	anchovy spp.	0.02	0.0000086	0.3	12.5	5.9	0.01	0.6
7/25/2001	Striped bass	3	8	SAV	0.01	0.0000086	0.3	12.5	5.9	0.01	0.6
8/28/2001	Striped bass	3	2	blue crab	0.01	0.0012699	97.1	50.0	40.0	0.69	68.6
8/28/2001	Striped bass	3	2	scales	1.70	0.0000187	1.4	50.0	40.0	0.21	20.7
8/28/2001	Striped bass	3	2	macro algae	0.03	0.0000187	1.4	50.0	20.0	0.11	10.7
9/25/2001	Striped bass	3	1	blue crab	0.03	0.0064071	100.0	100.0	100.0	2.00	100.0

10/9/2001	Striped bass	3	24	blue crab	7.90	0.1879259	46.7	70.8	71.4	0.84	84.5
10/9/2001	Striped bass	3	24	spot	5.75	0.1301445	32.4	29.2	5.9	0.11	11.3
10/9/2001	Striped bass	3	24	macro algae	3.98	0.0357046	8.9	8.3	1.7	0.01	0.9
10/9/2001	Striped bass	3	24	silver perch	1.09	0.0198964	4.9	12.5	2.5	0.01	0.9
10/9/2001	Striped bass	3	24	mummichog	0.61	0.0174434	4.3	12.5	3.4	0.01	1.0
10/9/2001	Striped bass	3	24	silverside spp.	0.53	0.0051785	1.3	8.3	3.4	0.00	0.4
10/9/2001	Striped bass	3	24	paleamonetes spp.	0.16	0.0040883	1.0	8.3	9.2	0.01	0.9
10/9/2001	Striped bass	3	24	unknown fish	0.13	0.0014990	0.4	8.3	1.7	0.00	0.2
10/9/2001	Striped bass	3	24	pipefish spp.	0.05	0.0004088	0.1	4.2	0.8	0.00	0.0
11/19/2001	Striped bass	3	3	mantis shrimp	0.01	0.5090090	50.9	66.7	50.0	0.67	67.1
11/19/2001	Striped bass	3	3	weakfish	15.07	0.2950450	29.5	33.3	7.1	0.12	12.2
11/19/2001	Striped bass	3	3	menhaden	8.73	0.1250000	12.5	33.3	7.1	0.07	6.5
11/19/2001	Striped bass	3	3	blue crab	3.70	0.0427928	4.3	33.3	28.6	0.11	10.9
11/19/2001	Striped bass	3	3	unknown fish	1.27	0.0281532	2.8	33.3	7.1	0.03	3.3
5/10/2001	Striped bass	4	2	blue crab	0.83	0.0091317	87.8	50.0	16.4	0.52	52.1
5/10/2001	Striped bass	4	2	polychaete spp.	16.30	0.0012605	12.1	50.0	81.8	0.47	47.0
5/10/2001	Striped bass	4	2	SAV	2.25	0.0000084	0.1	50.0	1.8	0.01	0.9
6/12/2001	Striped bass	4	1	blue crab	0.02	0.0153330	100.0	100.0	100.0	2.00	100.0
10/9/2001	Striped bass	4	6	silver perch	27.40	0.0035258	57.0	66.7	25.0	0.55	47.0
10/9/2001	Striped bass	4	6	blue crab	5.97	0.0015856	25.6	66.7	58.3	0.56	48.1
10/9/2001	Striped bass	4	6	spot	2.68	0.0010637	17.2	16.7	8.3	0.04	3.7
10/9/2001	Striped bass	4	6	scales	1.80	0.0000098	0.2	16.7	8.3	0.01	1.2
4/25/2001	Striped bass	>4	1	blue crab	0.02	0.0128421	84.7	100.0	35.6	1.20	60.2
4/25/2001	Striped bass	>4	1	polychaete spp.	36.60	0.0013684	9.0	100.0	53.4	0.62	31.2
4/25/2001	Striped bass	>4	1	crangon	3.90	0.0008772	5.8	100.0	9.6	0.15	7.7
4/25/2001	Striped bass	>4	1	sav	2.50	0.0000702	0.5	100.0	1.4	0.02	0.9
5/10/2001	Striped bass	>4	1	blue crab	0.20	0.0076794	100.0	100.0	100.0	2.00	100.0
5/25/2001	Striped bass	>4	1	blue crab	32.10	0.0073091	91.0	100.0	71.4	1.62	81.2
5/25/2001	Striped bass	>4	1	SAV	20.10	0.0004727	5.9	100.0	14.3	0.20	10.1
5/25/2001	Striped bass	>4	1	macro algae	1.30	0.0002545	3.2	100.0	14.3	0.17	8.7

10/9/2001	Striped bass	>4	3	blue crab	0.70	0.0025373	48.8	100.0	85.7	1.35	86.0
10/9/2001	Striped bass	>4	3	silver perch	6.80	0.0024129	46.4	33.3	4.8	0.17	10.9
10/9/2001	Striped bass	>4	3	mummichog	6.47	0.0002488	4.8	33.3	9.5	0.05	3.1
11/19/2001	Striped bass	>4	5	gizzard shad	0.67	0.0160172	95.9	40.0	42.9	0.56	81.9
11/19/2001	Striped bass	>4	5	mantis shrimp	144.92	0.0006013	3.6	20.0	28.6	0.06	9.5
11/19/2001	Striped bass	>4	5	American eel	5.44	0.0000531	0.3	20.0	14.3	0.03	4.3
11/19/2001	Striped bass	>4	5	SAV	0.48	0.0000287	0.2	20.0	14.3	0.03	4.3
5/10/2001	Bluefish	1	14	blue crab	0.26	0.003384	39.5	14.3	1.3	0.058	7.6
5/10/2001	Bluefish	1	14	crangon	1.69	0.002162	25.2	21.4	3.3	0.061	8.0
5/10/2001	Bluefish	1	14	polychaete spp.	1.08	0.002047	23.9	50.0	78.7	0.513	66.7
5/10/2001	Bluefish	1	14	paleamonetes spp.	1.02	0.000763	8.9	57.1	14.0	0.131	17.0
5/10/2001	Bluefish	1	14	pipefish spp.	0.38	0.000119	1.4	7.1	0.7	0.001	0.2
5/10/2001	Bluefish	1	14	macro algae	0.06	0.000086	1.0	14.3	1.3	0.003	0.4
5/10/2001	Bluefish	1	14	isopod spp.	0.04	0.000004	0.1	7.1	0.7	0.001	0.1
5/25/2001	Bluefish	1	5	paleamonetes spp.	0.00	0.001224	92.9	40.0	80.0	0.692	92.7
5/25/2001	Bluefish	1	5	unknown crab	0.60	0.000065	4.9	20.0	6.7	0.023	3.1
5/25/2001	Bluefish	1	5	crangon	0.03	0.000022	1.7	20.0	6.7	0.017	2.2
5/25/2001	Bluefish	1	5	SAV	0.01	0.000006	0.4	20.0	6.7	0.014	1.9
6/12/2001	Bluefish	1	39	paleamonetes spp.	0.00	0.008414	85.3	59.0	84.0	0.999	97.5
6/12/2001	Bluefish	1	39	silverside spp.	2.30	0.000844	8.6	10.3	6.5	0.015	1.5
6/12/2001	Bluefish	1	39	pipefish spp.	0.23	0.000150	1.5	5.1	0.7	0.001	0.1
6/12/2001	Bluefish	1	39	anchovy spp.	0.04	0.000122	1.2	5.1	1.0	0.001	0.1
6/12/2001	Bluefish	1	39	polychaete spp.	0.03	0.000113	1.1	10.3	4.1	0.005	0.5
6/12/2001	Bluefish	1	39	American eel	0.03	0.000094	1.0	2.6	0.3	0.000	0.0
6/12/2001	Bluefish	1	39	SAV	0.03	0.000049	0.5	5.1	0.7	0.001	0.1
6/12/2001	Bluefish	1	39	unknown fish	0.01	0.000047	0.5	5.1	0.7	0.001	0.1
6/12/2001	Bluefish	1	39	isopod spp.	0.01	0.000026	0.3	5.1	2.0	0.001	0.1
6/19/2001	Bluefish	1	4	paleamonetes spp	0.01	0.004816	100.0	75.0	100.0	1.500	100.0
7/10/2001	Bluefish	1	26	silverside spp.	1.13	0.002413	42.4	26.9	37.7	0.216	48.7
7/10/2001	Bluefish	1	26	American eel	0.74	0.001075	18.9	3.8	1.9	0.008	1.8

7/10/2001	Bluefish	1	26	paleamonetes spp	0.33	0.000813	14.3	38.5	30.2	0.171	38.6
7/10/2001	Bluefish	1	26	silver perch	0.25	0.000400	7.0	7.7	5.7	0.010	2.2
7/10/2001	Bluefish	1	26	anchovy spp.	0.12	0.000313	5.5	11.5	13.2	0.022	4.9
7/10/2001	Bluefish	1	26	unknown fish	0.10	0.000275	4.8	11.5	5.7	0.012	2.7
7/10/2001	Bluefish	1	26	menhaden	0.08	0.000225	4.0	3.8	1.9	0.002	0.5
7/10/2001	Bluefish	1	26	spot	0.07	0.000163	2.9	3.8	1.9	0.002	0.4
7/10/2001	Bluefish	1	26	SAV	0.05	0.000013	0.2	3.8	1.9	0.001	0.2
7/25/2001	Bluefish	1	17	paleamonetes spp.	0.00	0.005683	45.9	47.1	74.8	0.568	79.4
7/25/2001	Bluefish	1	17	silver perch	1.86	0.002886	23.3	29.4	10.2	0.099	13.8
7/25/2001	Bluefish	1	17	silverside spp.	0.95	0.001452	11.7	17.6	7.1	0.033	4.6
7/25/2001	Bluefish	1	17	weakfish	0.48	0.001344	10.9	5.9	0.8	0.007	1.0
7/25/2001	Bluefish	1	17	pipefish spp	0.44	0.000376	3.0	5.9	0.8	0.002	0.3
7/25/2001	Bluefish	1	17	unknown fish	0.12	0.000269	2.2	5.9	0.8	0.002	0.2
7/25/2001	Bluefish	1	17	anchovy spp.	0.09	0.000143	1.2	5.9	2.4	0.002	0.3
7/25/2001	Bluefish	1	17	spot	0.05	0.000143	1.2	5.9	0.8	0.001	0.2
7/25/2001	Bluefish	1	17	Atlantic needlefish	0.05	0.000072	0.6	5.9	1.6	0.001	0.2
7/25/2001	Bluefish	1	17	unknown	0.02	0.000018	0.1	5.9	0.8	0.001	0.1
8/28/2001	Bluefish	1	8	menhaden	0.01	0.012335	96.9	37.5	75.0	0.645	94.8
8/28/2001	Bluefish	1	8	silver perch	4.66	0.000397	3.1	12.5	25.0	0.035	5.2
9/18/2001	Bluefish	1	23	silver perch	0.15	0.007768	52.2	47.8	48.0	0.479	85.8
9/18/2001	Bluefish	1	23	spot	2.41	0.006323	42.5	8.7	8.0	0.044	7.9
9/18/2001	Bluefish	1	23	menhaden	1.96	0.000547	3.7	8.7	8.0	0.010	1.8
9/18/2001	Bluefish	1	23	unknown fish	0.17	0.000084	0.6	4.3	4.0	0.002	0.4
9/18/2001	Bluefish	1	23	blue crab	0.03	0.000056	0.4	4.3	12.0	0.005	1.0
9/18/2001	Bluefish	1	23	SAV	0.02	0.000056	0.4	8.7	8.0	0.007	1.3
9/18/2001	Bluefish	1	23	polychaete spp.	0.02	0.000042	0.3	8.7	12.0	0.011	1.9
9/25/2001	Bluefish	1	34	blue crab	0.01	0.004334	43.2	14.7	21.7	0.096	43.3
9/25/2001	Bluefish	1	34	menhaden	1.23	0.003045	30.4	17.6	26.1	0.100	45.1
9/25/2001	Bluefish	1	34	spot	0.86	0.001330	13.3	2.9	4.3	0.005	2.3
9/25/2001	Bluefish	1	34	unknown fish	0.38	0.000416	4.1	5.9	4.3	0.005	2.3

9/25/2001	Bluefish	1	34	silver perch	0.12	0.000395	3.9	2.9	8.7	0.004	1.7
9/25/2001	Bluefish	1	34	bluefish	0.11	0.000364	3.6	2.9	4.3	0.002	1.1
9/25/2001	Bluefish	1	34	anchovy spp.	0.10	0.000114	1.1	2.9	13.0	0.004	1.9
9/25/2001	Bluefish	1	34	SAV	0.03	0.000021	0.2	2.9	4.3	0.001	0.6
9/25/2001	Bluefish	1	34	macro algae	0.01	0.000005	0.1	2.9	4.3	0.001	0.6
9/25/2001	Bluefish	1	34	unknown	0.00	0.000001	0.0	2.9	8.7	0.003	1.2
10/9/2001	Bluefish	1	5	silver perch	0.00	0.002732	100.0	40.0	100.0	0.800	100.0
11/19/2001	Bluefish	1	2	menhaden	0.86	0.009833	90.9	50.0	50.0	0.705	70.5
11/19/2001	Bluefish	1	2	spot	5.00		9.1	50.0	50.0	0.295	29.5
5/10/2001	Bluefish	2	20	Atlantic croaker		0.001666	32.2	20.0	2.2	0.069	9.4
5/10/2001	Bluefish	2	20	silver perch	1.24	0.001241	24.0	10.0	1.1	0.025	3.4
5/10/2001	Bluefish	2	20	polychaete spp.	0.92	0.001051	20.3	55.0	89.4	0.603	82.3
5/10/2001	Bluefish	2	20	menhaden	0.78	0.000567	11.0	5.0	0.6	0.006	0.8
5/10/2001	Bluefish	2	20	unknown fish	0.42	0.000526	10.2	20.0	2.2	0.025	3.4
5/10/2001	Bluefish	2	20	paleamonetes spp.	0.39	0.000067	1.3	10.0	2.8	0.004	0.6
5/10/2001	Bluefish	2	20	macro algae	0.05	0.000034	0.7	5.0	0.6	0.001	0.1
5/10/2001	Bluefish	2	20	clam spp.	0.03	0.000013	0.2	5.0	0.6	0.000	0.1
5/10/2001	Bluefish	2	20	blue crab	0.01	0.000007	0.1	5.0	0.6	0.000	0.0
5/25/2001	Bluefish	2	5	menhaden	0.01	0.022332	96.4	20.0	16.7	0.226	56.5
5/25/2001	Bluefish	2	5	unknown fish	18.46	0.000670	2.9	20.0	16.7	0.039	9.8
5/25/2001	Bluefish	2	5	paleamonetes spp.	0.55	0.000169	0.7	20.0	66.7	0.135	33.7
6/12/2001	Bluefish	2	6	paleamonetes spp.	0.14	0.000852	36.0	16.7	63.2	0.165	49.6
6/12/2001	Bluefish	2	6	weakfish	0.67	0.000766	32.4	16.7	5.3	0.063	18.8
6/12/2001	Bluefish	2	6	unknown fish	0.60	0.000447	18.9	16.7	5.3	0.040	12.1
6/12/2001	Bluefish	2	6	unknown	0.35	0.000192	8.1	16.7	5.3	0.022	6.7
6/12/2001	Bluefish	2	6	scales	0.15	0.000085	3.6	16.7	15.8	0.032	9.7
6/12/2001	Bluefish	2	6	SAV	0.07	0.000021	0.9	16.7	5.3	0.010	3.1
5/25/2001	Weakfish	1	2	unknown fish	0.02	0.00623404	86.7	100.0	66.7	1.534	86.8
5/25/2001	Weakfish	1	2	spot	1.47	0.00085106	11.8	50.0	8.3	0.101	5.7
5/25/2001	Weakfish	1	2	polychaete spp.	0.20	6.383E-05	0.9	50.0	8.3	0.046	2.6

5/25/2001	Weakfish	1	2	amphipod spp.	0.02	4.2553E-05	0.6	50.0	16.7	0.086	4.9
6/12/2001	Weakfish	1	3	spot	0.01	0.00548204	44.2	33.3	0.7	0.150	15.9
6/12/2001	Weakfish	1	3	anchovy spp.	0.97	0.00374291	30.2	100.0	3.5	0.337	35.7
6/12/2001	Weakfish	1	3	mysid spp.	0.66	0.00151229	12.2	33.3	55.6	0.226	23.9
6/12/2001	Weakfish	1	3	amphipod spp.	0.27	0.00094518	7.6	33.3	37.5	0.150	15.9
6/12/2001	Weakfish	1	3	paleamonetes spp.	0.17	0.00071834	5.8	100.0	2.1	0.079	8.3
6/12/2001	Weakfish	1	3	juv. shrimp spp.	0.13	1.8904E-06	0.0	33.3	0.7	0.002	0.3
7/25/2001	Weakfish	1	1	silver perch	0.00	0.0133829	100.0	100.0	100.0	2.000	100.0
8/28/2001	Weakfish	1	1	silver perch	3.60	0.01231527	100.0	100.0	100.0	2.000	100.0
9/18/2001	Weakfish	1	10	blue crab	2.50	0.00316759	32.8	30.0	8.2	0.123	23.5
9/18/2001	Weakfish	1	10	anchovy spp.	0.60	0.0028322	29.3	40.0	18.0	0.189	36.3
9/18/2001	Weakfish	1	10	silver perch	0.53	0.00250213	25.9	10.0	1.6	0.028	5.3
9/18/2001	Weakfish	1	10	polychaete spp.	0.47	0.0007879	8.2	40.0	24.6	0.131	25.1
9/18/2001	Weakfish	1	10	amphipod spp.	0.15	0.00026618	2.8	10.0	45.9	0.049	9.3
9/18/2001	Weakfish	1	10	paleamonetes spp.	0.05	0.00010647	1.1	10.0	1.6	0.003	0.5
9/25/2001	Weakfish	1	9	blue crab	0.02	0.01212159	56.1	33.3	18.8	0.250	37.2
9/25/2001	Weakfish	1	9	anchovy spp.	2.14	0.00483608	22.4	44.4	62.5	0.377	56.2
9/25/2001	Weakfish	1	9	silver perch	0.86	0.00445924	20.6	11.1	6.3	0.030	4.4
9/25/2001	Weakfish	1	9	unknown	0.79	0.00012561	0.6	11.1	6.3	0.008	1.1
9/25/2001	Weakfish	1	9	shell	0.02	6.2806E-05	0.3	11.1	6.3	0.007	1.1
5/10/2001	Weakfish	2	16	polychaete spp	0.01	0.0168434	94.5	43.8	89.9	0.806	97.7
5/10/2001	Weakfish	2	16	blue crab	4.27	0.00064118	3.6	12.5	0.3	0.005	0.6
5/10/2001	Weakfish	2	16	amphipod spp.	0.16	0.00022195	1.2	12.5	9.7	0.014	1.7
5/10/2001	Weakfish	2	16	paleamonetes spp.	0.06	0.0001233	0.7	6.3	0.1	0.001	0.1
5/25/2001	Weakfish	2	6	anchovy	0.03	0.00111857	66.4	50.0	33.3	0.499	74.9
5/25/2001	Weakfish	2	6	paleamonetes spp.	0.33	0.00044183	26.2	16.7	33.3	0.099	14.9
5/25/2001	Weakfish	2	6	unknown fish	0.13	0.00010626	6.3	16.7	16.7	0.038	5.8
5/25/2001	Weakfish	2	6	crangon	0.03	1.6779E-05	1.0	16.7	16.7	0.029	4.4
6/12/2001	Weakfish	2	2	anchovy spp.	0.01	0.00293103	41.5	100.0	53.3	0.948	64.3
6/12/2001	Weakfish	2	2	paleamonetes spp.	0.85	0.00275862	39.0	50.0	40.0	0.395	26.8

6/12/2001	Weakfish	2	2	silver perch	0.80	0.00137931	19.5	50.0	6.7	0.131	8.9
7/10/2001	Weakfish	2	22	silver perch	0.40	0.00495541	38.6	40.9	26.2	0.265	40.7
7/10/2001	Weakfish	2	22	paleamonetes spp.	1.36	0.00245206	19.1	54.5	36.0	0.301	46.2
7/10/2001	Weakfish	2	22	spot	0.67	0.00170585	13.3	13.6	4.7	0.024	3.8
7/10/2001	Weakfish	2	22	menhaden	0.47	0.0015222	11.8	9.1	2.3	0.013	2.0
7/10/2001	Weakfish	2	22	blue crab	0.42	0.00095137	7.4	22.7	2.9	0.023	3.6
7/10/2001	Weakfish	2	22	anchovy spp.	0.26	0.00043184	3.4	13.6	3.5	0.009	1.4
7/10/2001	Weakfish	2	22	unknown	0.12	0.00043019	3.3	9.1	0.6	0.004	0.5
7/10/2001	Weakfish	2	22	unknown fish	0.12	0.00023495	1.8	4.5	16.3	0.008	1.3
7/10/2001	Weakfish	2	22	silverside spp.	0.06	8.2728E-05	0.6	4.5	0.6	0.001	0.1
7/10/2001	Weakfish	2	22	SAV	0.02	6.6182E-05	0.5	4.5	0.6	0.000	0.1
7/10/2001	Weakfish	2	22	skilletfish	0.02	8.2728E-06	0.1	4.5	0.6	0.000	0.0
7/10/2001	Weakfish	2	22	amphipod spp.	0.00	4.9637E-06	0.0	4.5	5.8	0.003	0.4
7/25/2001	Weakfish	2	14	silver perch	0.00	0.00597425	45.9	50.0	27.1	0.365	52.2
7/25/2001	Weakfish	2	14	unknown fish	1.61	0.00235269	18.1	28.6	6.8	0.071	10.2
7/25/2001	Weakfish	2	14	silverside spp.	0.64	0.00214121	16.4	21.4	10.2	0.057	8.2
7/25/2001	Weakfish	2	14	paleamonetes spp.	0.58	0.00128209	9.8	35.7	39.0	0.174	24.9
7/25/2001	Weakfish	2	14	penaeidea spp.	0.35	0.00047583	3.7	21.4	5.1	0.019	2.7
7/25/2001	Weakfish	2	14	unknown	0.13	0.00037009	2.8	7.1	1.7	0.003	0.5
7/25/2001	Weakfish	2	14	pipefish spp.	0.10	0.00018504	1.4	7.1	1.7	0.002	0.3
7/25/2001	Weakfish	2	14	blue crab	0.05	0.00013217	1.0	7.1	1.7	0.002	0.3
7/25/2001	Weakfish	2	14	anchovy spp.	0.04	0.00010574	0.8	7.1	6.8	0.005	0.8
8/28/2001	Weakfish	2	5	silver perch	0.03	0.00251442	48.6	40.0	22.2	0.283	35.7
8/28/2001	Weakfish	2	5	mantis shrimp	0.68	0.0011093	21.4	20.0	11.1	0.065	8.2
8/28/2001	Weakfish	2	5	macro algea	0.30	0.00044372	8.6	20.0	11.1	0.039	5.0
8/28/2001	Weakfish	2	5	blue crab	0.12	0.00014791	2.9	20.0	11.1	0.028	3.5
8/28/2001	Weakfish	2	5	anchovy spp.	0.04	0.0009614	18.6	60.0	44.4	0.378	47.6
9/18/2001	Weakfish	2	42	blue crab	0.26	0.00615652	33.9	54.8	17.6	0.282	44.4
9/18/2001	Weakfish	2	42	menhaden	1.79	0.00435061	23.9	4.8	1.0	0.012	1.9
9/18/2001	Weakfish	2	42	silver perch	1.26	0.00241992	13.3	16.7	5.0	0.031	4.8

9/18/2001	Weakfish	2	42	weakfish	0.70	0.00222456	12.2	2.4	0.5	0.003	0.5
9/18/2001	Weakfish	2	42	silverside spp.	0.65	0.00103758	5.7	14.3	3.5	0.013	2.1
9/18/2001	Weakfish	2	42	polychaete spp.	0.30	0.0009793	5.4	35.7	59.8	0.233	36.7
9/18/2001	Weakfish	2	42	anchovy spp.	0.28	0.00097191	5.3	35.7	11.6	0.060	9.5
9/18/2001	Weakfish	2	42	unknown	0.28	9.0296E-05	0.5	2.4	0.5	0.000	0.0
9/18/2001	Weakfish	2	42	SAV	0.03	2.4626E-05	0.1	2.4	0.5	0.000	0.0
9/25/2001	Weakfish	2	43	blue crab	0.01	0.00557908	56.7	37.2	25.0	0.304	52.0
9/25/2001	Weakfish	2	43	anchovy spp.	1.47	0.00196285	19.9	44.2	34.8	0.242	41.3
9/25/2001	Weakfish	2	43	silver perch	0.52	0.00130856	13.3	9.3	4.3	0.016	2.8
9/25/2001	Weakfish	2	43	mantis shrimp	0.34	0.00068965	7.0	4.7	2.2	0.004	0.7
9/25/2001	Weakfish	2	43	macro algae	0.18	7.9575E-05	0.8	2.3	1.1	0.000	0.1
9/25/2001	Weakfish	2	43	silverside spp.	0.02	7.5154E-05	0.8	4.7	2.2	0.001	0.2
9/25/2001	Weakfish	2	43	SAV	0.02	5.305E-05	0.5	2.3	1.1	0.000	0.1
9/25/2001	Weakfish	2	43	goby spp.	0.01	2.6525E-05	0.3	2.3	1.1	0.000	0.1
9/25/2001	Weakfish	2	43	unknown	0.01	2.6525E-05	0.3	4.7	2.2	0.001	0.2
9/25/2001	Weakfish	2	43	polychaete spp.	0.01	2.2104E-05	0.2	2.3	3.3	0.001	0.1
9/25/2001	Weakfish	2	43	amphipod spp.	0.01	1.3262E-05	0.1	7.0	19.6	0.014	2.3
9/25/2001	Weakfish	2	43	paleamonetes spp.	0.00	6.1892E-06	0.1	2.3	1.1	0.000	0.0
10/9/2001	Weakfish	2	4	menhaden	0.00	0.01618329	69.8	25.0	16.7	0.216	29.8
10/9/2001	Weakfish	2	4	blue crab	4.45	0.00536412	23.1	50.0	66.7	0.449	62.0
10/9/2001	Weakfish	2	4	silver perch	1.48	0.00163651	7.1	25.0	16.7	0.059	8.2
11/19/2001	Weakfish	2	8	anchovy spp.	0.45	0.00989237	83.7	87.5	78.6	1.420	94.8
11/19/2001	Weakfish	2	8	polychaete	2.88	0.00120063	10.2	25.0	9.5	0.049	3.3
11/19/2001	Weakfish	2	8	menhaden	0.35	0.00033875	2.9	12.5	2.4	0.007	0.4
11/19/2001	Weakfish	2	8	spot	0.10	0.00029158	2.5	12.5	2.4	0.006	0.4
11/19/2001	Weakfish	2	8	blue crab	0.09	8.576E-05	0.7	25.0	4.8	0.014	0.9
11/19/2001	Weakfish	2	8	amphipod spp.	0.03	4.288E-06	0.0	12.5	2.4	0.003	0.2
5/10/2001	Weakfish	3	10	weakfish	0.00	0.00273936	49.5	10.0	1.2	0.051	0.2
5/10/2001	Weakfish	3	10	polychaete spp	1.03	0.00148936	26.9	50.0	66.7	0.468	2.2
5/10/2001	Weakfish	3	10	paleamonetes spp.	0.56	0.00119681	21.6	10.0	17.9	0.039	0.2

5/10/2001	Weakfish	3	10	amphipods	0.45	5.3191E-05	1.0	10.0	13.1	0.014	0.1
5/10/2001	Weakfish	3	10	blue crabs	0.02	5.3191E-05	1.0	10.0	1.2	0.002	0.0
5/25/2001	Weakfish	3	1	paleamonetes spp.	0.02	0.00352941	100.0	100.0	100.0	2.000	100.0
6/12/2001	Weakfish	3	2	paleamonetes spp.	1.20	0.01377543	90.1	100.0	78.3	1.683	89.3
6/12/2001	Weakfish	3	2	blue crab	4.30	0.00096108	6.3	50.0	2.2	0.042	2.2
6/12/2001	Weakfish	3	2	anchovy spp.	0.30	0.00032036	2.1	100.0	6.5	0.086	4.6
6/12/2001	Weakfish	3	2	unknown	0.10	0.00016018	1.0	50.0	2.2	0.016	0.9
6/12/2001	Weakfish	3	2	juv. Shrimp spp.	0.05	8.009E-05	0.5	50.0	10.9	0.057	3.0
7/10/2001	Weakfish	3	12	paleamonetes spp.	0.03	0.00557225	35.0	50.0	78.2	0.566	67.1
7/10/2001	Weakfish	3	12	menhaden	2.18	0.00483709	30.4	41.7	6.7	0.155	18.3
7/10/2001	Weakfish	3	12	blue crab	1.89	0.00277014	17.4	8.3	0.8	0.015	1.8
7/10/2001	Weakfish	3	12	silver perch	1.08	0.0021735	13.7	41.7	10.9	0.102	12.1
7/10/2001	Weakfish	3	12	unknown fish	0.85	0.00028767	1.8	8.3	0.8	0.002	0.3
7/10/2001	Weakfish	3	12	anchovy spp.	0.11	0.00017899	1.1	8.3	1.7	0.002	0.3
7/10/2001	Weakfish	3	12	SAV	0.07	8.3104E-05	0.5	8.3	0.8	0.001	0.1
7/25/2001	Weakfish	3	14	spot	0.03	0.01791045	70.0	50.0	8.7	0.393	39.3
7/25/2001	Weakfish	3	14	unknown	8.40	0.00298507	11.7	50.0	4.3	0.080	8.0
7/25/2001	Weakfish	3	14	silver perch	1.40	0.00287846	11.3	50.0	17.4	0.143	14.3
7/25/2001	Weakfish	3	14	polychaete spp.	1.35	0.00127932	5.0	50.0	65.2	0.351	35.1
7/25/2001	Weakfish	3	14	paleamonetes spp.	0.60	0.00053305	2.1	50.0	4.3	0.032	3.2
8/28/2001	Weakfish	3	2	silver perch	0.25	0.00731675	80.3	100.0	50.0	1.303	71.0
8/28/2001	Weakfish	3	2	blue crab	2.75	0.00146335	16.1	50.0	16.7	0.164	8.9
8/28/2001	Weakfish	3	2	SAV	0.55	0.00033258	3.6	100.0	33.3	0.370	20.1
9/18/2001	Weakfish	3	20	spot	0.13	0.00488257	53.2	10.0	1.3	0.055	23.0
9/18/2001	Weakfish	3	20	silver perch	1.95	0.00150233	16.4	15.0	2.0	0.028	11.6
9/18/2001	Weakfish	3	20	blue crab	0.60	0.00143973	15.7	20.0	2.7	0.037	15.5
9/18/2001	Weakfish	3	20	anchovy spp	0.58	0.00069608	7.6	20.0	6.7	0.029	12.0
9/18/2001	Weakfish	3	20	menhaden	0.28	0.00040062	4.4	5.0	0.7	0.003	1.1
9/18/2001	Weakfish	3	20	polychaete spp.	0.16	0.00015524	1.7	10.0	83.9	0.086	36.0
9/18/2001	Weakfish	3	20	paleamonetes spp.	0.06	5.7589E-05	0.6	5.0	2.0	0.001	0.6

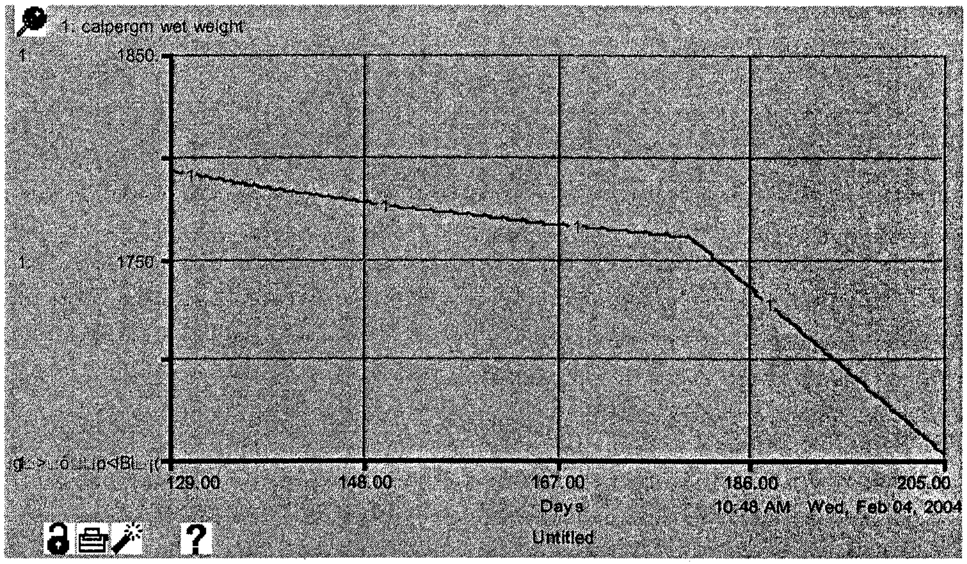
9/18/2001	Weakfish	3	20	unknown fish	0.02	3.7558E-05	0.4	5.0	0.7	0.001	0.2
9/25/2001	Weakfish	3	8	blue crab	0.02	0.02125812	55.6	50.0	29.4	0.425	65.0
9/25/2001	Weakfish	3	8	menhaden	8.88	0.01062906	27.8	12.5	5.9	0.042	6.4
9/25/2001	Weakfish	3	8	mantis shrimp	4.44	0.00476062	12.5	25.0	23.5	0.090	13.7
9/25/2001	Weakfish	3	8	macro algae	1.99	0.00062876	1.6	25.0	11.8	0.034	5.1
9/25/2001	Weakfish	3	8	anchovy spp.	0.26	0.000509	1.3	25.0	17.6	0.047	7.3
9/25/2001	Weakfish	3	8	spotted trout	0.21	0.00023953	0.6	12.5	5.9	0.008	1.2
9/25/2001	Weakfish	3	8	silverside spp.	0.10	0.00017965	0.5	12.5	5.9	0.008	1.2
10/9/2001	Weakfish	3	1	anchovy spp.	0.08	0.001365	100.0	100.0	100.0	2.000	100.0
11/19/2001	Weakfish	3	1	unknown fish	0.50	0.000807	100.0	100.0	100.0	2.000	100.0
5/10/2001	Weakfish	>3	6	menhaden	0.38	0.00606257	51.2	50.0	1.4	0.263	22.6
5/10/2001	Weakfish	>3	6	blue crabs	9.37	0.00325458	27.5	50.0	8.6	0.180	15.6
5/10/2001	Weakfish	>3	6	polychaete spp	5.03	0.00226537	19.1	66.7	86.8	0.706	60.9
5/10/2001	Weakfish	>3	6	silver perch	3.50	0.00022654	1.9	16.7	0.5	0.004	0.3
5/10/2001	Weakfish	>3	6	SAV	0.35	3.2362E-05	0.3	33.3	0.9	0.004	0.3
5/10/2001	Weakfish	>3	6	isopod spp.	0.05	5.3937E-06	0.0	16.7	0.9	0.002	0.1
5/10/2001	Weakfish	>3	6	amphipod spp.	0.01	4.315E-06	0.0	16.7	0.9	0.002	0.1
9/25/2001	Weakfish	>3	3	weakfish	0.01	0.01250068	98.1	33.3	25.0	0.410	49.0
9/25/2001	Weakfish	>3	3	blue crab	15.40	0.00016235	1.3	66.7	50.0	0.342	40.8
9/25/2001	Weakfish	>3	3	anchovy spp.	0.20	8.1173E-05	0.6	33.3	25.0	0.085	10.2

Appendix 15. This appendix contains nocturnal diet percentages for each month used to construct trophic ecology figures. Samples where n<2 were not included in analysis or list. Data is listed in order species, age and then sample month. Other consists of all unknown, unknown fish, rock, scales, and all floral components. Prey groups included in benthic and pelagic categories are listed in appendix 12.

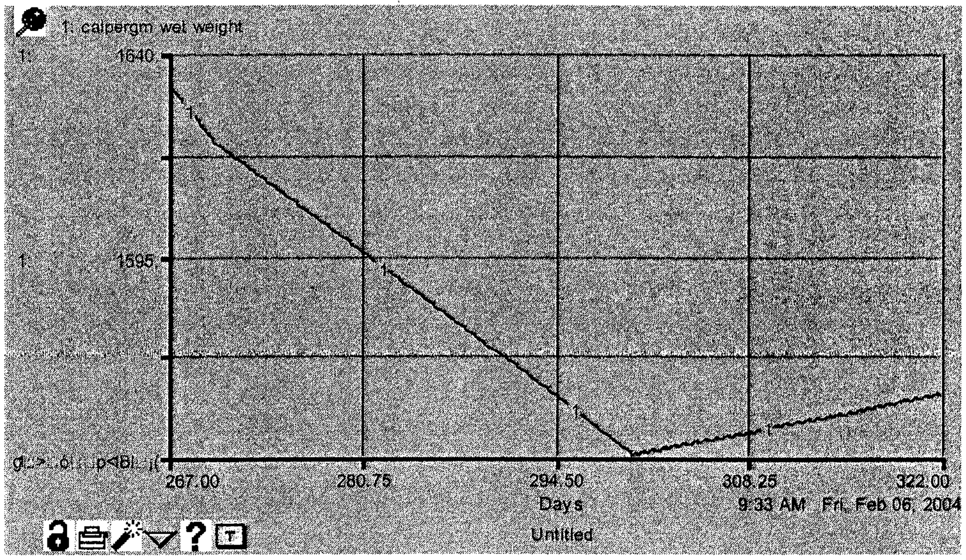
Species	Month	Age	Benthic	Pelagic	Other
Striped Bass	6	1	83	9	8
Striped Bass	7	1	88	11	1
Striped Bass	10	1	74	26	0
Striped Bass	11	1	80	12	8
Striped Bass	5	2	100	0	0
Striped Bass	6	2	100	0	0
Striped Bass	7	2	82	15	3
Striped Bass	10	2	100	0	0
Striped Bass	11	2	94	0	6
Striped Bass	5	3	94	0	6
Striped Bass	6	3	100	0	0
Striped Bass	7	3	91	0	9
Striped Bass	10	3	89	1	10
Striped Bass	11	3	55	42	3
Striped Bass	10	4	100	0	0
Striped Bass	10	4<	100	0	0
Striped Bass	11	4<	4	96	0
Bluefish	5	1	99	0	1
Bluefish	6	1	89	10	1
Bluefish	7	1	67	30	3
Bluefish	9	1	79	17	4
Bluefish	10	1	100	0	0
Bluefish	5	2	33	65	2
Bluefish	6	2	36	32	32
Weakfish	6	1	70	30	0
Weakfish	9	1	74	25	1
Weakfish	5	2	97	2	1
Weakfish	7	2	71	16	13
Weakfish	9	2	61	39	0
Weakfish	10	2	30	70	0
Weakfish	11	2	13	87	0
Weakfish	5	3	53	47	0
Weakfish	7	3	76	17	7
Weakfish	9	3	75	23	2
Weakfish	5	3<	49	51	0
Weakfish	9	3<	1	99	0

Appendix 16: This appendix contains the seasonal energy densities (cal g $^{-1}$ wet weight) of striped bass during the spring and fall model periods as determined by Hartman (1993). Spring is listed at the top of the page and fall at the bottom as labeled.

Spring
Age 2

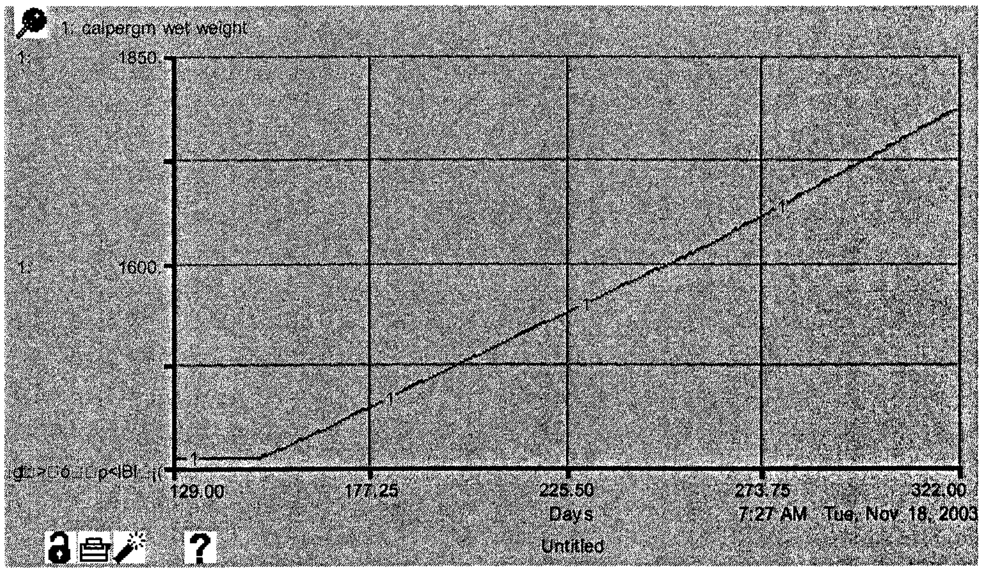


Fall
Average
Age 2 and 3+

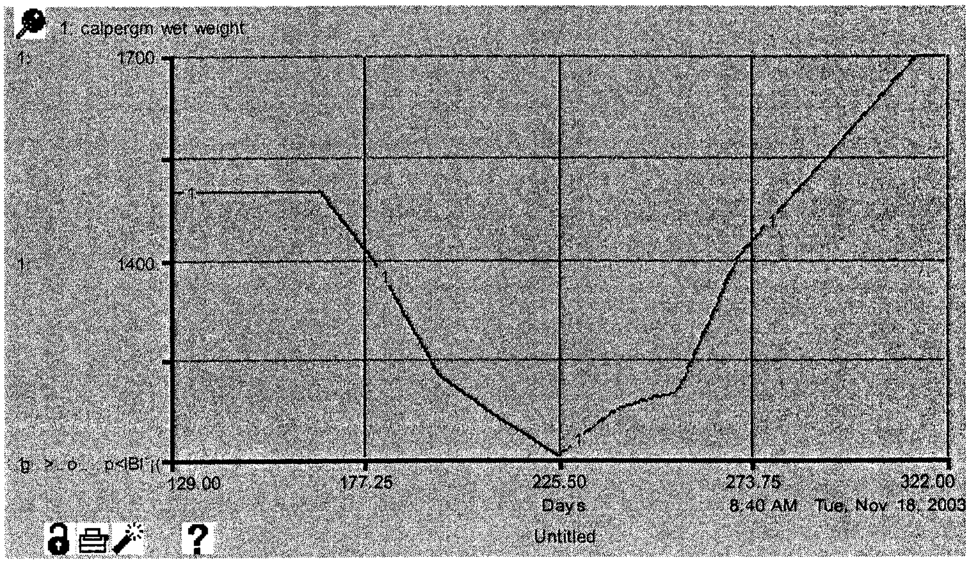


Appendix 16: Appendix 16 continues on this page. It contains the seasonal energy densities (cal g $^{-1}$ wet weight) of bluefish and weakfish during the modeled period as determined by Hartman (1993). Bluefish is listed at the top of the page and weakfish at the bottom as labeled.

Bluefish
Age 1+



Weakfish
Age 1+



Appendix 17. This appendix contains littoral zone piscivore growth model's text and equations.

Overall Description

These dynamic bioenergetic models estimate the growth of bluefish and weakfish from May to November based upon field-determined nocturnal rations within a vegetated mesohaline littoral zone collected in 2001. Striped bass required two models one for spring and early summer model and another for fall. Two models were necessary because fish disappeared from the study area during warm water periods in late summer. Model construction required estimates of trophic demand and capacity determined by Hartman and Brandt (1995b) in laboratory experiments. Estimating piscivore growth based on field-determined daily ration provides for growth comparisons with other models and a functional means of comparing habitats that will aid in the identification and preservation of essential fish habitat.

Run Method Euler
Time step = one day
DT=.25 day

Assumptions and caveats

1. Gut content of predator reflects feeding in habitat in which predator was captured.

2. Stomach content of average fish per day can be estimated by multiplying stomach fullness index (grams food source per gram predator per day) by the average mass of predator.

3. Differential energy content of prey is adequately dealt with through application of varied evacuation rates attained from literature.

4. Low piscivore daytime abundances in littoral zone indicated that fish are in deeper water during daylight hours.

5. Predation occurs equally across nocturnal period and thus the initial and final levels of food in the stomach are equal across this time period.

6. Trophic dynamics of piscivores are adequately described by and not biased by sampling regime.

7. Temporal energy densities average age of bluefish was assumed to be 1, weakfish were assumed to be age 2, striped bass spring model assumed to be age 2, and striped bass fall model energy densities were the average of age 2-3≤. Assumptions were based on fish size and life history.

Forcing functions

1. All stomach content is based on field-determined stomach analysis. Prey content categories that follow are self-explanatory.

2. Nocturnal hours (darkness hours) and daylight hours (cos daylight)

3. Average littoral temperature (T ave Lit), littoral nocturnal temperature (T Lit noc), and deep-water temperatures (temp deep)

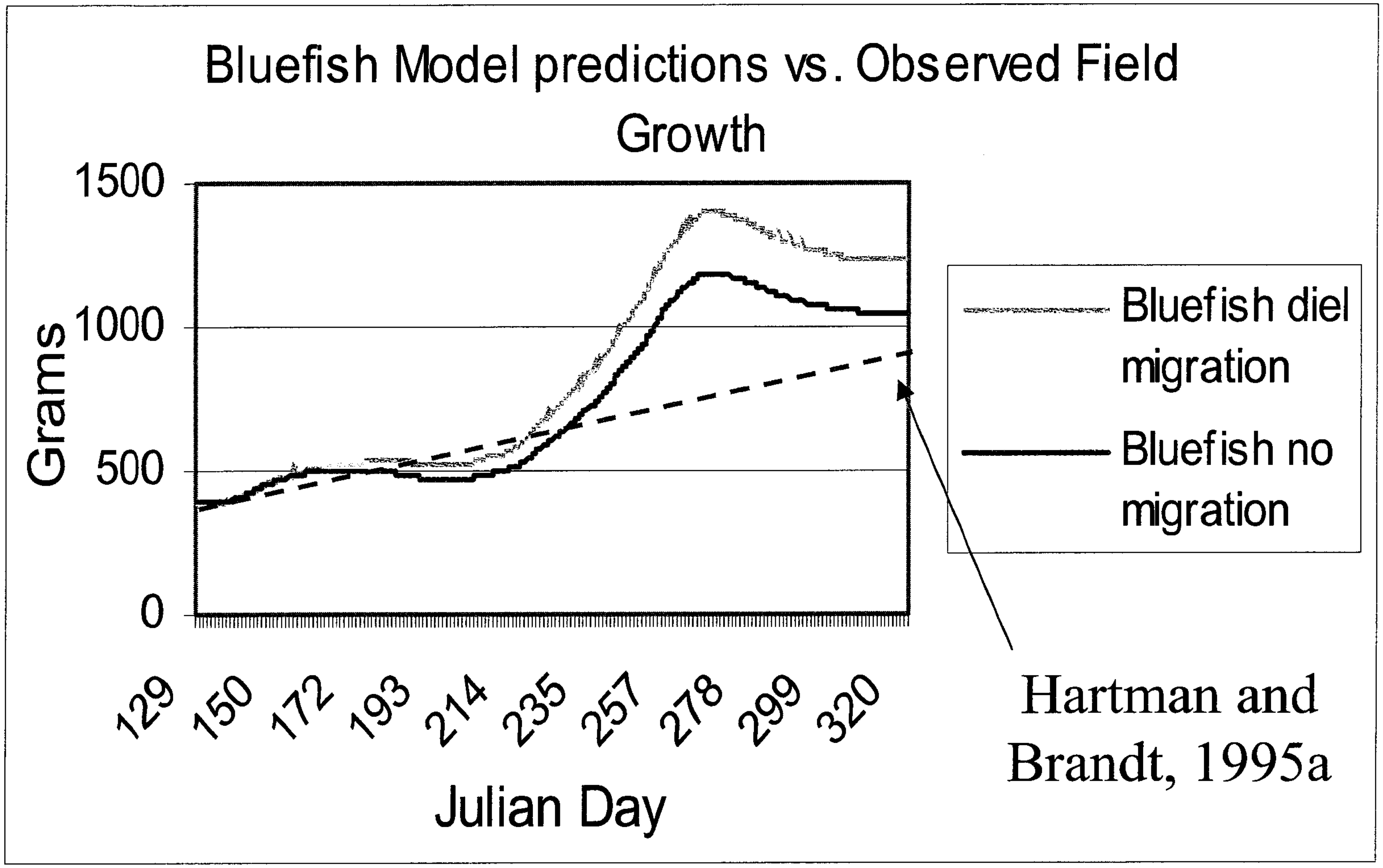
4. Piscivores' energy content over time (cal per gm wet weight)

Prey groups:

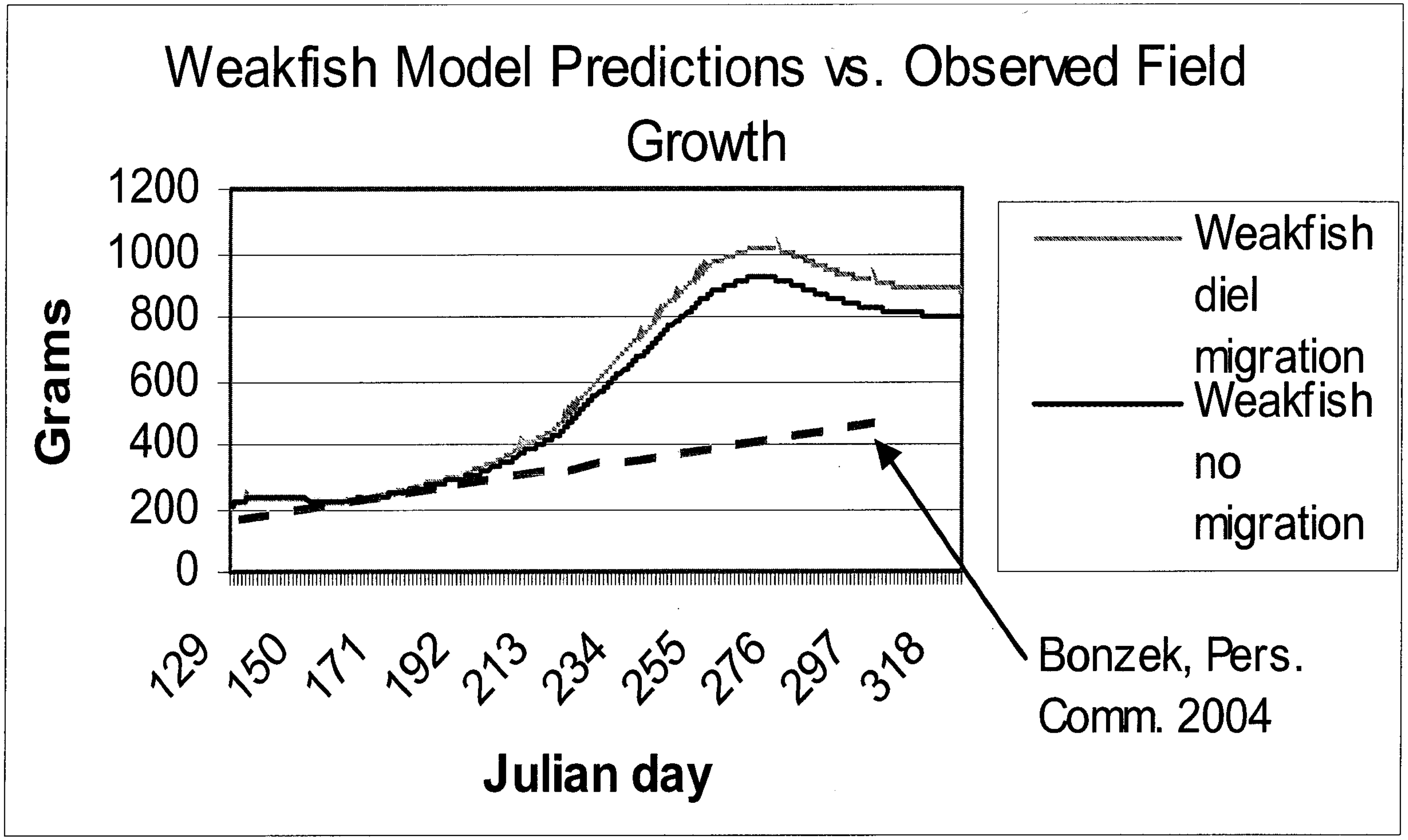
The following chart explains the content of taxa based prey groups. Species-specific groups are not included.

Prey Group	Species
Anchovy	Anchovy species
Silversides	Silverside species
Benthic Fish	Gobies, blennies, skillet fish, tonguefish
Unknown fish	Unknown fish parts
Small crustaceans	Amphipod, isopod, and mysid species
Shrimp	Crangon, paleamonetes, panaeidean
Unknown	Unknown crustacean parts
Polycheates	Polycheate species

Appendix 18. This appendix contains graphs of bluefish predicted growth based on littoral rations and those determined in the field.


Bluefish Model predictions vs. Observed Field Growth
1500
1000
500
0
Grams
129
150
172
193
214
235
257
278
299
320
Julian Day
Bluefish diel migration
Bluefish no migration
Hartman and Brandt, 1995a

Appendix 19. This appendix contains graphs of weakfish predicted growth based on littoral rations and those determined in the field.


Weakfish Model Predictions vs. Observed Field Growth
Grams
1200
1000
800
600
400
200
0
129
150
171
192
213
234
255
276
297
318
Julian day
Weakfish diel migration
Weakfish no migration
Bonzek, Pers. Comm. 2004

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